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The Journal of the Council appears *three times a year*, and three numbers form a volume. It includes, in addition to general articles, reviews, and bibliography, the special papers previously issued in the series of *Publications de Circonstance*.

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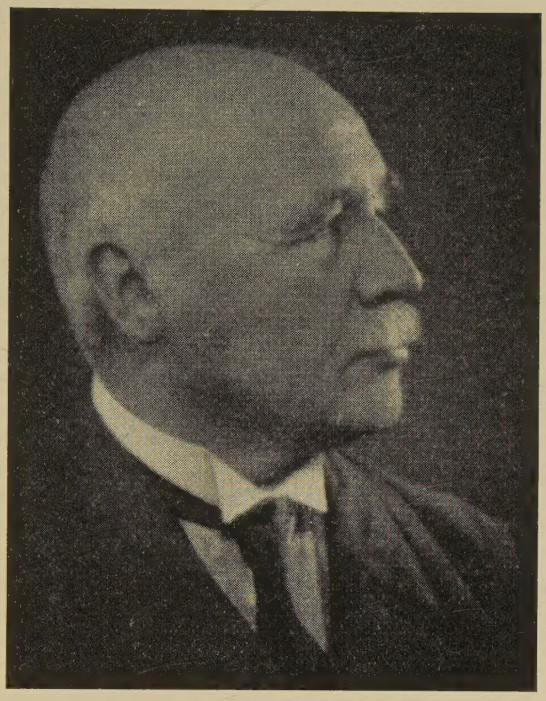


Knut Dahl.

1871—1951.

KNUT DAHL passed away on 11. June 1951. On 28. October he would have been 80 years of age, as he was born on that day in 1871.

He grew up in Hakadal, near Oslo, where his father was the manager of an estate. Living in a land of vast forests, lakes, and rivers, K n u t D a h l quite naturally became a first-rate shot and a clever angler, and acquired an intimate knowledge of game and fish.

Entering the University in Oslo in 1889 he studied zoology. These studies were interrupted in 1893, however, when he was given the opportunity of conducting an expedition to South

Africa and north-west Australia to collect animals for the University Museum. In 1896 he returned, bringing with him rich and valuable material for the museum. Amongst this he brought one mammal, one snake, and one frog species new to science. The results of his expedition have appeared in a number of publications, among them his own work "In Savage Australia". When one reads this book, so full of information and precise knowledge, so alive and so diverse, one is amazed to think that the author was then a young man of only 25. His book has remained an important source of information on the little-known Arnhem Land of north-west Australia.

After his return to Norway in 1896 D a h l completed his university studies and became leader of the Biological Station in Trondheim. In 1903 he moved to Bergen as J o h a n H j o r t' s assistant and was for a number of years engaged in marine fishery research. The first decade of this century was a rich period in fishery development, and D a h l played an important part in it and contributed several valuable publications. Following H j o r t' s advice, he took up special research on salmon and trout. In 1911 he was given his doctor's degree for a treatise on "The Age and Growth of Salmon and Trout as shown by their Scales", a work certainly known to everyone who has studied salmon and trout. In this paper D a h l proved very clearly that the scales of these salmonoid fishes reflect their entire life cycle, their river abode, their feeding years in the sea, and their spawning.

D a h l had now entered a field in which he continued to work till his death. In the course of years he published a great number of valuable works on freshwater fisheries research — on salmon, trout, char, and grayling, on bottom organisms, and the productivity of lakes. He discovered that two of our river systems contained landlocked salmon (the "Blege" or dwarf salmon).

D a h l' s work was experimental as well as descriptive. The funds available to his Freshwater Research Laboratory, established at Oslo in 1912, were very limited, and only permitted experimental work on a modest scale. Reading his papers to-day, one is struck by the small numbers of fish or fish eggs in each experiment, and yet he arrived at important general conclusions. He was able to arrange his experiments so as to answer distinct questions; he drew his conclusions with great care, allowing himself to be guided by his common sense and his vast knowledge of animal behaviour. Many of his discoveries have been rediscovered from a very much larger

material in recent years. Thus his discovery that trout fry from large eggs grow faster than fry from small eggs has been confirmed by recent experiments in Canada and Sweden.

K n u t D a h l' s experiments had a modest purpose; he wanted to learn sufficient to be able to teach fishery biology at the Norwegian Agricultural High School. But his works eventually became known all over the world and inspired others to extensive research.

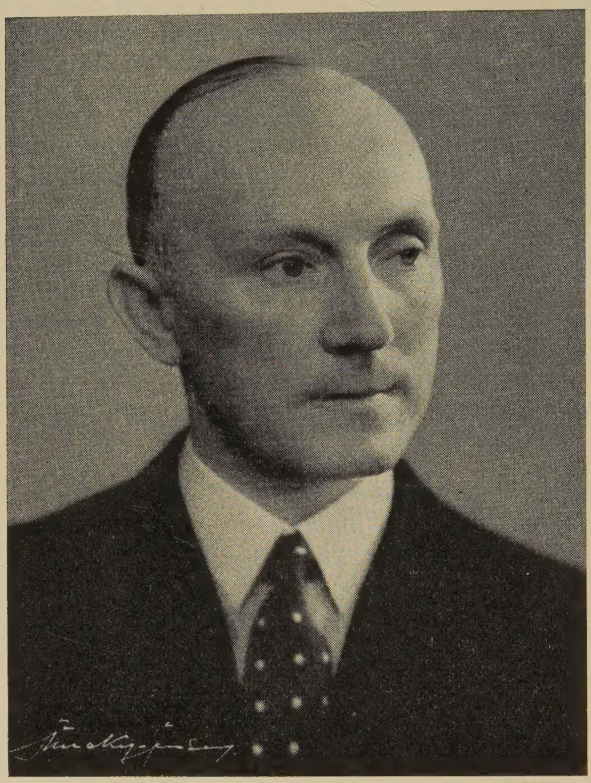
In recent years D a h l spent most of his time on the one species that had always been closest to his heart, the salmon. In 1935 he started tagging experiments on a large scale, to study the migration of salmon as they approach their spawning grounds, and at the same time he collected an enormous quantity of statistical data on the seasons for salmon fishing at various places on the coasts and in the fjords. This work is still incomplete, but will be published eventually.

When K n u t D a h l passed away, all who knew him felt they had lost a good friend. His was a friendly nature, and his deep-rooted love of humanity was coupled with a keen sense of humour. These happy qualities made up the charm which we all knew and valued, and which drew all men to him.

For many years he took part in the annual meetings of the International Council for the Exploration of the Sea, and was chairman of the Salmon and Trout Committee from 1945 to 1950.

He will be deeply missed by his numerous friends.

Sven Sømme.



Poul Jespersen.

1891—1951.

IN the death of P o u l J e s p e r s e n the International Council has lost a regular and devoted attendant at its meetings and science has lost a distinguished worker with great experience of the sea.

J e s p e r s e n was born on 18th March 1891 at Næsbyhoved near Odense, the son of V a l d e m a r J e s p e r s e n who owned the estate of Næsbyhoved. On leaving school in Odense in 1910 he went to the University at Copenhagen where in his first year as a student he came under the influence of J o h s. S c h m i d t. He was given the opportunity of examining the marine collections made on the "Thor" and on the first expeditions sent out to study the life history of the eel. This probably determined

the direction his life's work was to take and in 1913 Jespersen sailed on his first cruise in the schooner "Margrethe" to search for the larvae of the eel in the Sargasso Sea; on this expedition the vessel was wrecked two days before Christmas.

During the 1914—18 war, while still a student at the University he also worked at the Carlsberg Laboratory on oceanic fish and plankton, becoming *Magister scientiarum* in 1917, and in the same year senior assistant at the plankton laboratory of Kommissionen for Danmarks Fiskeri- og Havundersøgelser then directed by C. H. Ostenfeld. He was eventually to become head of that laboratory, succeeding the distinguished plankton worker Ove Paulsen.

Jespersen spent much of his life on the sea. In 1920 he accompanied Schmidt in the motor schooner "Dana", and during the next two years on the cruise of the research vessel S. S. "Dana II" to the Atlantic and Pacific. Subsequently he accompanied the Carlsberg Foundation's oceanographical circumnavigation of the world in 1928—30 on S. S. "Dana II". In between these expeditions and after his return Jespersen made many cruises in Faroe, Iceland, and Greenland waters for fisheries research, sailing for the last time in S.S. "Dana III" in 1947.

His publications in marine biology were numerous and covered a wide field. He was especially a copepod systematist, but he wrote also papers on the systematics of oceanic fishes and larval eels, and on the life histories of the halibut and the eel. He made a number of general studies of the abundance of zooplankton, and detailed observations on the part it plays as food for herring. For the most comprehensive observations on the food of herring in Danish waters he gained his Doctor's degree in 1928. Jespersen's experiences at sea and his first-hand observations on the volumes of the catches in the plankton nets no doubt inspired him to collect together the very valuable data he has recorded on the quantities of macroplankton in different parts of the oceans.

Jespersen was a very modest man, and on meeting him for the first time one could not gauge the breadth of his interests. Not only was he a very experienced and sound marine biologist; he was also an ornithologist of considerable distinction. His lifelong interest in birds began in his boyhood days, when in 1907 at the age of sixteen he became a member of the then recently established Danish Ornithological Society. For over forty years he was a regular attendant of the society's meetings and excursions, being its Secretary from 1911 onwards, and becoming its President in 1941, a distinction of which he was very

proud. He published many scientific papers and popular articles on the distribution of Danish breeding birds, and on his many oceanographical cruises made observations on the distribution of oceanic birds. Combining this work with his research on plankton he showed the connexion between the abundance of sea birds and that of the plankton on which they feed.

He was actively interested in the preservation of bird life, being a member of the board of management of the Danish Society for Nature Preservation and since 1928 Danish delegate to the International Committee for Bird Preservation; he was also a corresponding member of the Swedish Fauna Society.

In 1948, at the invitation of Prof. F. Bernard, Jespersen spent six months in Algiers as Professor in the "Chaire d'Actualités Scientifiques" at the University, where he lectured on "Migrations of Marine Animals", and did research on the food of the sardine and anchovy. While in Algeria he took the opportunity of analysing observations available on the migrations of the stork in northern Africa. In 1949 and 1951 he was working in Paris with Prof. Louis Fage at the Muséum National d'Histoire Naturelle on collections of copepods brought back from Greenland and Arctic seas by the expeditions of the "Pourquoi Pas?".

For a number of years he has edited with great care and energy the valuable series of plankton identification sheets published by the International Council, and future workers on plankton will remember his name with gratitude.

On the death of Harald Blegvad in 1951, Jespersen was appointed provisionally as Secretary General of the International Council, an appointment which was to be formally ratified at the meeting held in October 1951 in Amsterdam. He was taken ill at the beginning of the meeting and died on 20th December 1951. The Council has thus lost a familiar figure and a loyal friend whose wide experience of the world and knowledge of languages would have made him invaluable in the post to which he was elected.

In his own country his services to science were recognized by his appointment as a Knight of the Dannebrog.

In 1919 Jespersen married Miss Rola Wohlleben of Stige, near Odense, and they had one daughter. To them goes the deepest sympathy of Poul Jespersen's many friends, whose visits to Copenhagen were made so enjoyable by their charming company and generous hospitality.

F. S. Russell.

An Automatic Collector for Water and Plankton Samples.

By

C. H. Roberts,

Ministry of Agriculture and Fisheries, London.

FOR some purposes in marine research and often in rivers, lakes, and estuaries it may be desirable to collect chemical and other samples continuously for many days. A particular application is where pollution is suspected. Many difficulties could be overcome by using a collecting instrument which is completely automatic and which could work without supervision. Such a collector would not demand the use of a special research ship but could be installed upon a lightship, a cross-Channel packet, or trawler, and would save time and money.

Such an instrument has been made and will now be described. It is completely automatic and when in use, does not demand the attention of anyone. It could operate successfully hundreds of miles away from the nearest human being. It will record temperatures and collect and preserve samples for the subsequent examination of the following contents:— plankton; dissolved gases, such as oxygen and carbon dioxide; mineral salts, such as magnesium and calcium compounds; salinity; organic matter. It switches itself on at the desired time and sea water is pumped through a group of sample bottles. When these are thoroughly flushed out the appropriate chemical reagents or preservatives are added and the bottles are sealed. The "electric brain" then stops the machine, which is now ready for the next cycle of collection.

When plankton is collected, a measured amount of sea water is passed through a special filter and the plankton container is then sealed after the addition of formaldehyde.

The present machine will run unattended for 33 days and can collect 200 groups of samples or 6 groups of samples a day. There would be no difficulty in collecting 400 groups instead of 200; it would merely be necessary to add more magazines of sample bottles. By adding another clock the sampling time may be extended to 66 days. Samples can be

collected at any desired intervals of time — regular or irregular. Sampling times are infinitely variable from one group every 15 minutes to one group every 24 hours.

One can, if desired, cut out the time-switch and start the collector by pressing a button. It would then operate automatically and switch itself off. This hand-switch might be preferable to a clock if the machine were installed in a research vessel or cross-Channel packet, where it could be pressed by the Officer of the Watch at the appropriate times. If the inlet pipe were connected to a seacock it would not be necessary to stop the ship to collect samples and these could be collected at speed. As the "electric brain" could control two or more inlets it would be possible to collect both surface samples and samples collected from a point near the keel. A machine could be mounted upon a cross-Channel packet and adjusted to collect samples from the surface and at a depth of 5 metres. The time-switch could be set to sample every 5 nautical miles and the instrument would be started by a ship's Officer pressing a button on leaving harbour. Another button would be pressed to stop it on arrival at the ship's destination.

One might collect samples for plankton, dissolved oxygen, salinity, phosphates, and temperature. If one sampled at two different depths on various routes the costs per round journey would be, for example:—

Folkestone—Boulogne (every 5 miles)	£ 1-0-0 per round trip
Newcastle—Bergen (every 5 miles)	£ 16-0-0 per round trip
Southampton—New York (every 30 miles).	£ 24-0-0 per round trip

In these estimates the author has allowed for the cost of the collector, electric current, and chemical reagents. He has not allowed for installation charges nor for the cost of the analyses.

The machine already constructed is primarily designed to collect samples at one or two depths when mounted in a moving ship but it is easy to adapt it for vertical series by either of the following means. A long rubber pipe of 1-inch internal diameter with a strainer and weight at the inlet end would be lowered deep into the sea. One would sample at this depth for about 10 minutes. Then the tube would be pulled up 10 metres and the performance repeated. One would shorten the pipe again and sample at another depth.

A much better method, however, would be to lower 4 or 5 tubes into the sea, each at a different depth. Each tube would have its own pump and all of them would be driven from a common shaft by one motor. By this means one could sample simultaneously from 4 or 5 different depths. An investigation is being made into the possibility of towing the inlet tube at moderate depths down to 20 fathoms and at speeds up to 15 knots.

As the collector is completely self-contained it could be left unattended for periods up to 66 days, upon a lightship or an isolated lighthouse. If one used a number of synchronized machines it would be possible to carry out simultaneous observations at widely separated

positions at sea. For example, one might obtain useful results if automatic collectors were mounted upon six lightships in the southern North Sea, all six adjusted to collect samples at the same time.

The cost of the control unit, water-meter, pumping assembly, and photographic recorder would be about £ 120. A group of three sample bottles, for dissolved oxygen, salinity, and plankton samples, would cost about £ 4 each.

On an actuarial basis the cost of a collector and its operation would be:—

(a) The cost of a 100-group sampler is about £ 550.
(b) Yearly depreciation at 10 % would amount to £ 55 per annum.
(c) Cost of chemical reagents and electric current would amount to 1/- per group of three samples.

The cost of collecting 5,000 samples a year would, therefore, be about £ 300. The saving that might be effected would depend upon how the machine is used. In a research ship the saving would not be great, but if used in a cross-Channel packet one could collect a very large amount of data at a very low cost.

The accuracy of the instrument should be comparable with that attained by existing methods, but for dissolved oxygen and plankton samples, the accuracy might even be greater, because if one uses the Winkler process for oxygen, manipulative errors are avoided, and plankton is filtered from an accurately measured volume of water.

The machine could also be used in freshwater work for the detection and estimation of pollution. At present much pollution occurs, for obvious reasons, at those times when no one is watching the river, at night, at week-ends, and on public holidays. A collector could sample an effluent by day and by night and one can imagine few things that would deter a potential polluter more than the knowledge that such an instrument was at work just below his factory.

Disadvantages of the Collector. It is unorthodox and its use would demand a technique very different from that used with more conventional methods. It is bulky and complicated. But as all delicate parts are sealed in a watertight box in an atmosphere of dry nitrogen, it should be reasonably reliable. Bulk might be reduced by using much smaller sample bottles and by adopting micro methods of analysis.

It might be claimed that the machine does not solve the problem of transporting the scientific staff to the place where the research work will be done. But, if properly used, this collector might partly solve the problem; being automatic it would need only a small scientific staff to work it and as it could operate at speed, it would not be necessary to use a special research ship for some of the work, as this could be delegated to a commercial vessel.

It might be said that it would collect samples at such a speed that the staff could never cope with them. But by relieving the staff from the tedium of collecting samples, it would not only release scientists for the examination of these samples but would allow more time to be given to other researches.

Description of the Collector.

There are three units in the collector, consisting of an electric brain which starts and stops the machine and exercises an overall control; a pumping unit comprising an electrically driven water pump and a header tank; a number of magazines loaded with sample bottles of special design.

Electric Brain of Automatic Collector (Figures 1 and 3). At the desired time the clock closes the contacts A and B and the electromagnetic coil C is energized. This pulls home two armatures one of which closes contacts which start the centrifugal pump and the geared Klaxon motor, and the other one of which rocks contacts A and B away from the clock hand and holds coil C circuit closed.

The electric pump now drives water through a group of sample bottles. If plankton is being collected in addition to ordinary water samples, the filtered water from a plankton bottle passes through a water-meter.

Whilst this is taking place a cam on the rotary switch is slowly approaching contacts D and E and after 6 minutes have passed, it closes these, and current passes through the stepper switch and through a pair of contacts on the uniselector switch which corresponds with the group of sample bottles being flushed out with water. The current then passes through a fusible plug which melts, releases the plunger, adds the appropriate reagents, and seals a group of sample bottles (Figure 2).

The rotary switch cam continues to move and closes contacts F and G and current flows through the coil of the uniselector switch, pulling home the armature.

The moving cam then closes contacts H and I, energizing coil J and after a short interval, coil K. This opens contacts Q and R_1, which are normally closed, and breaks the circuit.

The following events now happen. The clock contacts return to their normal open position; the pump stops; the motor-driven rotary switch stops; the uniselector switch arm moves one division forward, ready for the next cycle.

When the sliding contact of the uniselector has reached the 25th fixed contact current can flow, not only through a fusible plug, but also through the stepper switch relay which pulls this switch forward one notch, thereby bringing the second bank of uniselector fixed contacts into circuit.

The operation of the electromagnetic relays M, N, O, and P, which are in the "uniselector-fusible plug" circuit, will be obvious from the diagram, which shows that each bank of fixed contacts has its own relay. In the diagram it will be seen that bank 1 and electromagnetic relay M are in operation. When bank 2 comes into operation through the energizing of uniselector stud 25, then electromagnetic relay N comes into circuit and relay M is switched out.

When plankton is being collected the sealing of the bottle actuates a camera which photographs the dial of the water-meter, thus recording

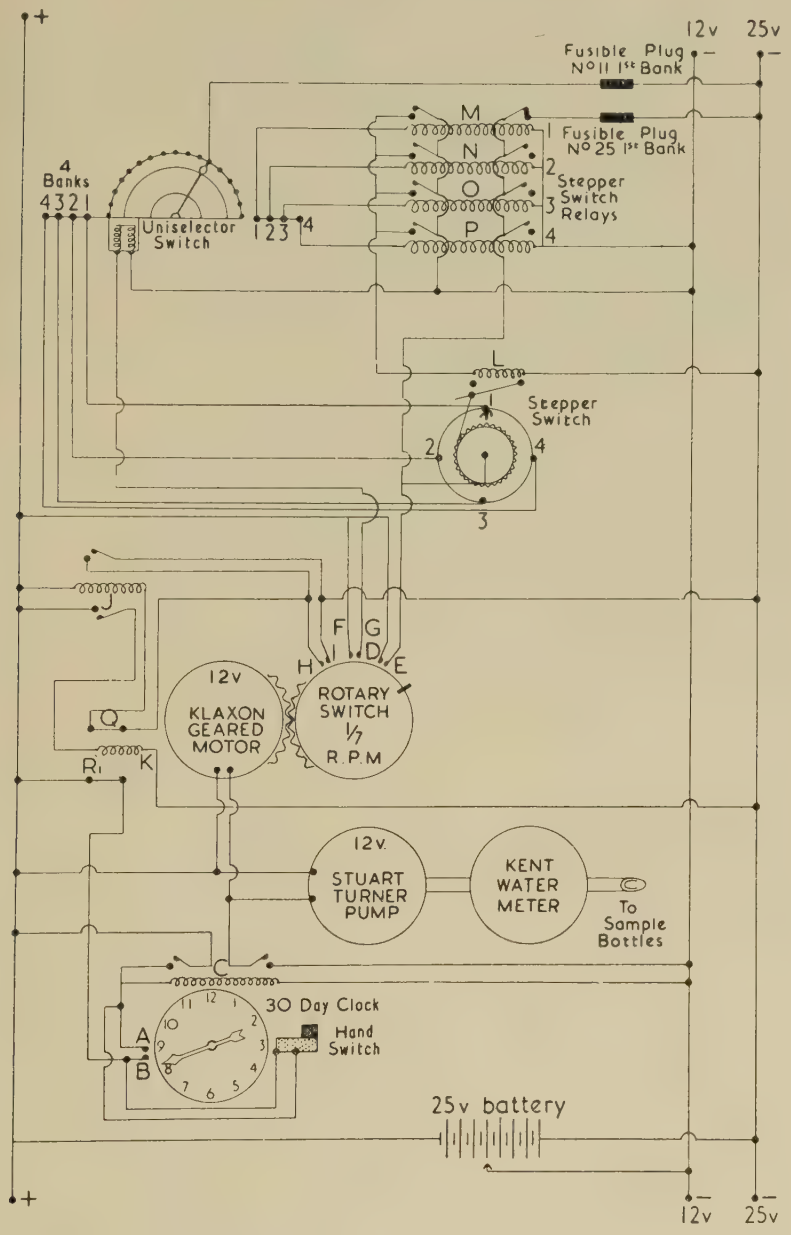


Figure 1. Theoretical Circuit of the Electric Brain.

the number of gallons that have passed through the filter. It also photographs the mercury column of a sensitive thermometer mounted in the inlet pipe. The camera may be of special design such as the "single-shot"

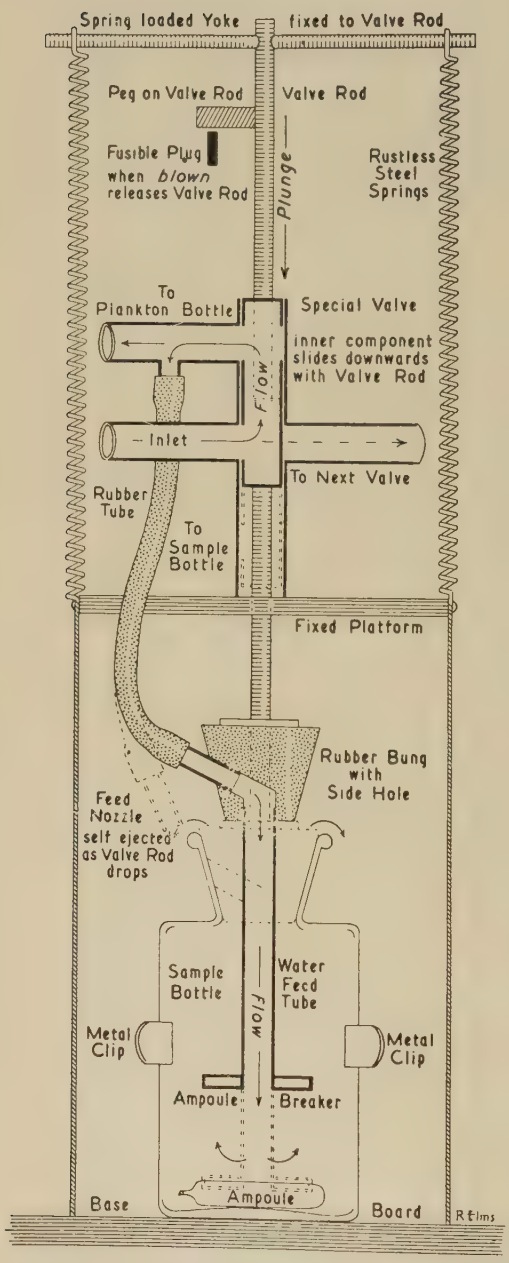


Figure 2. Sample Bottle for Dissolved Oxygen.

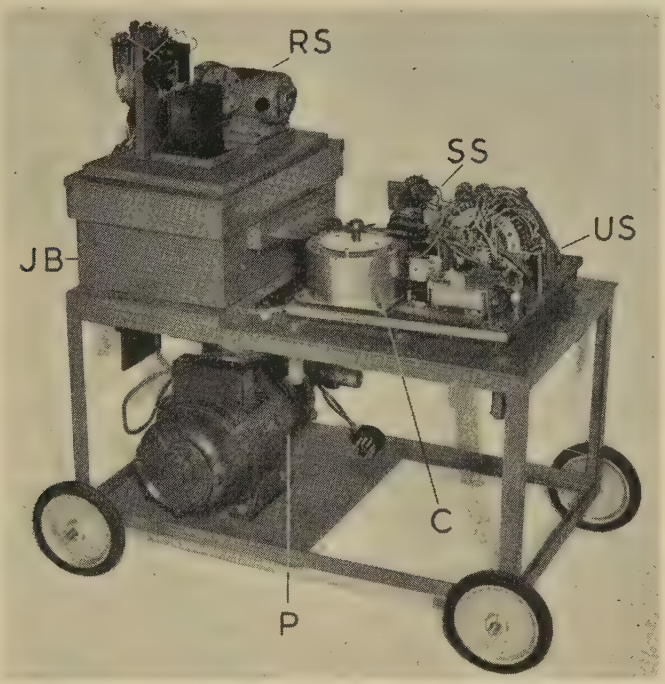
Avimo or it may be an 8 mm. cine-camera slowed down to about 5 frames a second. In both cases one would use polarized light to cut out reflections and Kodak Super X reversal film. It might be of interest to photograph also a thermometer recording air temperatures.

The amount of water passing might be roughly adjusted by means of a resistance on the motor of the rotary switch and may be varied from about 500 to 2,000 gallons per hour.

Pumping Assembly (Figure 3). This comprises an inlet pipe from the sea and an electrically driven pump. The inlet pipe may be joined to a seacock or on to the condenser intake in a steamship or on to the cooling water intake of a Diesel-engined ship. A filter, preferably of the easily cleaned Thornycroft type, is fitted in the pipeline to keep out everything except small organisms. Alternatively, for use when stationary, a flexible rubber hose-pipe is used. This would have a filter and footvalve at its outer end.

On the intake side of the pump there is a larger header tank of at least 5 gallons capacity to ensure that the pump is always submerged. So-called "self-priming" pumps sometimes fail to start after being idle. This is due to air-locks caused by the emission of gases from phyto-plankton. But by using a larger header tank and a good self-priming pump this difficulty is overcome.

Magazine Units and Sample Bottles (Figures 2 and 4). In the early models water was pumped to waste and no special valves were employed to direct the incoming



RS Rotary switch
SS Stepper switch
US Uniselector switch
C Clock
P Pump
JB Junction box

Figure 3. The Electric Brain and Centrifugal Pump.

water from one group of bottles to the next. This system had the merit of great simplicity but limited the number of groups that could be collected to 10, before re-loading. In the present collector specially designed slide valves are employed and the number of groups that can now be collected runs into hundreds, and it is possible to leave the machine unattended for long periods before re-loading. The specially designed slide valve has negligible friction, is cheap to make, and offers little resistance to the flow of water.

The sample bottles are of two types, one for samples for chemical analyses and the other for plankton samples. A different design may be used for salinity samples. The first bottle resembles that used in the earlier machines as experiments have not been able to suggest any improvements. The working principle is illustrated in Figure 2. In the "ready" position the plunger assembly is held out, against the tension of two springs, by means of a fusible plug. At the required moment an electric current ignites this plug, which falls to pieces and releases the plunger, which is pulled downwards to seal the bottles and to add the chemical reagents by breaking the ampoules. The reagents in these ampoules are sealed in an atmosphere of nitrogen during manufacture (British Drug Houses Ltd.).

The fusible plugs are made by overlapping two strips of brass and soldering these together. The soldered joint is then covered with a heating

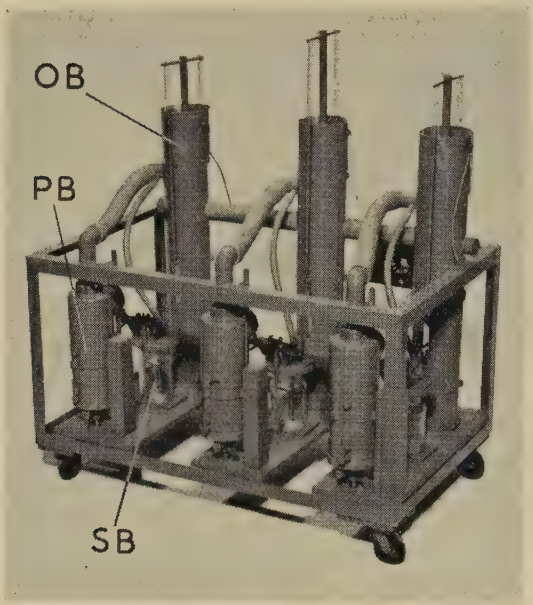


Figure 4. The Magazine Unit.
OB Oxygen bottle
PB Plankton bottle
SB Salinity bottle

compound and this, in turn, is covered with a match compound which is ignited by means of a resistance wire which becomes red-hot when an electric current passes through it. When the heating compound is ignited by the match it melts the solder and the two brass strips fall apart. The downward movement of the plunger-stopper assembly operates the slide valve as well as sealing the bottle and adding the reagents.

Where there is much pollution, as in estuaries near big cities, it is possible to carry out preliminary oxidation (Winkler process for dissolved oxygen). This is done by interposing a Rotherham "Delay". The plunger would seal the oxygen bottle and break into it ampoules containing sodium azide and sulphuric acid. Five minutes later the "Delay" would release another spring-loaded plunger which would break ampoules containing manganous chloride and potassium iodide plus caustic potash.

The plankton bottle is made from a fuel filter and has the merit that it can be dismantled in a few seconds, without any tools. The area of gauze is 24 square inches but this may be increased, if desired, by using several filters mounted in parallel or by the simple device of lengthening the filter by welding on an extra length of tube and by extending the inner filtration unit. Without unduly increasing the size of a filter it would be possible to attain a filtering area of 200 square inches.

It would be advisable, of course, to experiment with a variety of internal filters apart from the conventional miller's gauze. It would be interesting also to test bakelized paper disks made by Streamline Filters,

pock-marked metal disks made by Metafilters, and aerofoil-section wire filters made by Purolators. It would be easy to test the relative efficiency of all four types by joining them in parallel and feeding in sea water from a common inlet pipe. The outlet from each filter should be measured by a water-meter. Such a test would soon show which type of filter collected the most plankton with the least resistance.

The water from a plankton bottle would be measured by passing it through a Kent water-meter which has an error of under $^1/_2$ % and which can register flows as low as 3 gallons an hour and up to 10,000 gallons an hour. The inlet to the plankton bottle is connected to the special valve shown in Figure 2, and the outlet valve is a flap-valve held open by a catch when in the sampling position. When the plunger of the dissolved oxygen bottle is released the inner part of the slide valve plunges downwards and seals the plankton bottle inlet. The moving slide valve then trips the catch which holds open the outlet flap-valve and closes the bottle. This valve holds an ampoule of formaldehyde which is broken into the contents of the bottle, thus preserving the plankton for subsequent examination. The breaking of the ampoule and the sealing of the bottle both occur at the same instant. Finally, the slide valve, when released, opens a passage to the next group of sample bottles.

A Simplified Miniature Sample Collector.

If one does not desire to collect plankton but only samples for chemical analyses it becomes possible to modify the design of the automatic collector to obtain a smaller, cheaper, and simpler machine. Such an instrument has been made and is now under test. This machine is completely automatic, weighs about 20 pounds, and is the size of a large attaché case (14 inches long, by 16 inches high, by 4 inches wide). It has been found possible to dispense with much electrical equipment, including the pump. The instrument costs about £ 30.

This collector will work completely submerged, and for marine research could be used in several ways. It could be suspended in the sea by a thin cable and operated by messengers released by a clock mounted in the ship, lightvessel, or buoy. It might be enclosed in a box and connected in the condenser water circuit of a ship for collecting samples automatically and at speed. It could be mounted inside a kite and towed in the sea at the required depth. In this case it might be worked by the rotator from a "Cherub" ship's log. This rotator has ample power and makes 900 revolutions per nautical mile. By using suitable gears it should be possible to sample at any desired interval.

It might also be useful in freshwater research where it could help in survey work and in the collection of samples for the detection of pollution in rivers, lakes, and estuaries. Its small size should be an advantage in this work, where the transport of apparatus has always been a problem. In pre-war days workers in this field almost always used automobiles but nowadays, in many countries, such a method is

hampered by restrictions and high costs. But miniature collectors could easily be carried on public vehicles or trains. These collectors might be used in a variety of ways on rivers and a few suggestions are given below.

A biologist would proceed to a river where pollution had been reported and would place one collector above the suspected factory and one below it. The scientist would then leave the instruments to collect water samples and would proceed with his biological investigations. At the end of the day he would re-load the machines, which would continue to collect samples throughout the night. By this method one scientist, using two collectors, could do an amount of work which would need three men if more conventional methods were used. Furthermore, the cost would be much less.

At present most pollutions are undetected in their early stages, when it is easy to start effective remedial measures. If a number of collectors were used in all large rivers, and moved about as experience dictated, such pollutions would be detected very rapidly. If used on an English watershed it is estimated that six collectors would keep a close watch on the condition of all the rivers. In many cases it would not be necessary for a scientist to accompany the collectors as these could be sent by train, ready for use, to some trustworthy local man who would place them in the desired positions. When the collecting cycle was finished, this man would send the instruments back to the central laboratory for analysis and would replace them, if necessary, with fresh units. It is estimated that the cost of using twelve machines in this way would be under £ 800 per annum. This figure includes the cost of the instruments, depreciation, upkeep, and travelling expenses, for which latter item £ 1 per week has been allocated to each machine. But it does not include the cost of analysing the samples. Twelve instruments would collect samples at about the same rate as twenty scientists and would do the work at a small fraction of the cost of the more conventional methods.

The author wishes to thank the Government Chemist for the help and advice given so freely by members of his staff in the design and construction of the two collectors. Thanks are also due to Mr. P e r r y-m a n and Mr. E l m s, of the Ministry's staff, the former for many useful suggestions and for assembling the plankton collector, and the latter for preparing the photographs and drawings.

The Use of Radio-active Carbon (C^{14}) for Measuring Organic Production in the Sea.

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1. Introduction.

As on land, so in the sea autotrophic plants are the basis of all life. Sessile plants, however, live on a narrow fringe along the coasts only. If we wish to consider the amount of matter produced annually by the plants of the sea, we must therefore confine our attention to the plankton algae, which are found everywhere in the upper water-masses of the sea. It is the organic matter synthesized by the plankton algae out of purely inorganic substances by means of light which directly and indirectly serves as food for all organisms in the sea, from the smallest bacteria to the largest whale.

As the constantly increasing number of human beings on our globe requires greater and greater quantities of food, and as the food production on land can be but little increased, we must consider the sea as an important reserve.

It is therefore of great importance to be able to estimate the amount of the annual production by the plants of the sea. In recent years one has repeatedly come across figures according to which the annual production of organic matter in the sea is nearly ten times that of the production on land. These figures originate from Rabinowitch (1945), who has collected his data mainly from American sources (Riley, 1938, 1939, 1941, and Seiwell, 1935).

Whereas, according to Rabinowitch, the land annually fixes $1{\cdot}9\times10^{10}$ tons of carbon, a value originally calculated by Schroeder (1919), the sea is said to fix $15{\cdot}5\times10^{10}$ tons of carbon.

Both Riley's and Seiwell's figures for the production of organic matter in the tropical Atlantic seem incredible, even before determinations were made by the "Galathea" Expedition, and, indeed,

in what follows it will be shown that even the order of magnitude is wrong.

Before the "Galathea" Expedition put to sea in October 1950, the production of organic matter in the oceans must therefore be considered as completely unknown. Only values for the production in a few northern coastal waters had been determined by reliable methods, methods which it would normally be impossible to use on the open sea. It is therefore highly significant that the expedition was provided with equipment for determining the production of matter by phytoplankton by an entirely new method. This method, which has taken the radioactive carbon isotope C^{14} into its service, has now been used by the "Galathea" Expedition in all the oceans. It has proved applicable with equal certainty whether the productivity of the sea area was very high or extremely low. A basis has now been established for an estimate of the production of matter in the oceans, at any rate on broad lines.

2. Methods previously used for Determining the Production of Matter in the Sea.

The first attempts at determining the production of organic matter in a coastal region were made in the English Channel (A t k i n s, 1922, 1923). Until then scientists had had to content themselves with investigations of the magnitude of the standing crop of plants. Observations of this kind are of course of great interest in themselves. In many respects they are, however, a poor basis for a determination of the production of matter.

To take an example from the land; if immediately before the harvest we compare the quantities of matter found per square metre of surface in a cornfield and a wood, by far the greatest amount of organic matter will be found in the wood. Here the amount of matter has accumulated during a long series of years, whereas all the organic matter in the cornfield has been produced in a single season. If the production of matter in the two localities is to be determined in such a way that comparison is possible, we must determine the amount of organic matter produced in a year through photosynthesis, thus getting the gross production. If we deduct from this quantity the respiration of the plants during the year, we shall get the net production. Both the gross and the net production can be used for comparison of the productivity in the two areas.

The quantity of matter in the plankton in a sea area at a certain time cannot, of course, be compared directly with the amount of matter in the land regions mentioned above, as the matter in the sea has been produced in a very short period, often only a few days. If the production of matter by the plankton always took place at the same rate, it would of course be possible to compare the productivity of the plankton in the various areas on the basis of the amount of plankton present. However, this is not the case at all. Temperature, light, and amount of nutrient salts are of decisive importance for the rate of production.

Furthermore, the consumption of phytoplankton by the animals is involved. It is therefore evident from these considerations that it may be quite illusory to deduce the total organic production from the amount of matter in phytoplankton.

As mentioned above, the first investigations of the actual production of matter by phytoplankton in the sea area were made by Atkins (1922 and 1923) in the English Channel. He proceeded partly by determining the loss of carbon dioxide, and partly by observing the loss of phosphate under 1 sq.m. of surface from the end of winter to the height of summer. As the amounts of these substances which had disappeared must have been used to build up vegetable matter, the production of matter in six months could be calculated from the values found. Atkins was aware that he was dealing only with minimal values, as it was not possible to consider, for example, the phosphate regenerated during the period and utilized again, or the exchange of CO_2 with the atmosphere. Other workers have used the method elsewhere — for instance, Kreps and Verjbinskaya (1932) in the Barents Sea. For the English Channel Cooper (1933) based his estimate on the change in the content of oxygen and nitrate. The method of N- and P-metabolism has also been used in the Kattegat, between the Baltic and the North Sea (Steemann Nielsen, 1940). The peculiar hydrographical conditions prevailing there, in which the euphotic surface layer is replaced six times a year by water from deeper layers without a simultaneous downward transport of surface water, give much surer values for the N- and P-assimilation than usual in the sea. In addition to the content of nitrate in the water rising from the depths, the content of ammonia was also measured.

Finally a similar study in the south-western part of the North Atlantic (Seiwell, 1935) should be mentioned. Estimates of the undersaturation of oxygen in a layer below the photosynthetic zone in conjunction with calculations of the exchange of oxygen with the over- and underlying water-masses through turbulence were used as a measure of the production of matter by plankton algae. In this Seiwell assumed that the annual amount of organic matter was finally oxidized in this particular layer. According to Redfield (1933), however, the oxygen deficiency in the water-layer arose at a time when the water-masses forming this layer were nearer the surface much farther north. Seiwell's improbably high production value for tropical water in the western part of the Atlantic cannot therefore be correct.

Riley and Gorgy (1948) used the vertical distribution of oxygen in the Sargasso Sea. The net total production of organic matter was estimated by standard physical oceanographical methods.

The only earlier method which directly gives the production of matter by phytoplankton is that introduced by Gran. Water samples from various depths are put into bottles and replaced at the different depths, normally for 24 hours. The oxygen production, which is an expression of the photosynthesis, is determined by measuring the amount of oxygen present at the start and end of the experiment. By simultaneously

suspending bottles wrapped in black material, one can also determine the respiration. Apart from Gaarder and Gran's investigations (1927) and those of Gran and Thompson (1930) the method has been little used, as it is only suitable in sea areas with a large production of organic matter. Marshall and Orr (1930) used this method to measure the spring plankton production in a Scottish fiord, and Steemann Nielsen (1932, 1937, and 1951) also used it at various places in Danish waters. In two localities the production was measured 2 to 4 times a month for 1 to 2 years. In 1932 the method was subjected to an experimental test.

In America a modification of the method has been used in both eutrophic and oligotrophic regions (Riley, 1938, 1939, 1941a, 1941b), although in the latter with little success, as will be shown in Section 6. In these American investigations it was often not the actual photosynthesis by phytoplankton which was measured, but something else.

3. The C^{14} Method for Determining the Intensity of Photosynthesis.

The equation for photosynthesis, $CO_2+H_2O+\text{energy} = (CH_2O)+O_2$, shows that it is of no importance whether this process is measured through the assimilation of CO_2, through the production of O_2, or through the formation of organic matter. In the C^{14} method the incorporation of the tracer in the organic matter is used as the starting point. A definite amount of $C^{14}O_2$ is added to sea water for which the content of $CO_{2\,(total)}$ is known. If we assume that $C^{14}O_2$ is assimilated by the plankton algae only through photosynthesis and that $C^{14}O_2$ is assimilated photosynthetically at the same rate as $C^{12}O_2$ — as is, however, certainly not the case (see later) — by determining the content of C^{14} in the plankton algae after the experiment, we also determine the total amount of carbon assimilated; it is only necessary to multiply the amount of C^{14} found by a factor corresponding to the ratio between $CO_{2\,(total)}$ and $C^{14}O_2$ in the water at the beginning of the experiment.

The amount of C^{14} assimilated is determined by measuring the β-radiation from the plankton, which is retained by a collodion filter. On broad lines, this is the method by which the intensity of photosynthesis in a quantity of water containing phytoplankton can be measured. In practice there are, however, numerous factors to be considered.

(a) Preparation of Glass Containers for Sea Water containing Definite Quantities of $C^{14}O_2$.

C^{14} was supplied from Oak Ridge, U. S. A., in the form of $BaCO_3$ with 4·79 per cent. of the carbon in the form of C^{14}. As $BaCO_3$ is insoluble, this substance cannot be used directly. Artificial sea water was therefore prepared which had a nearly normal content of total CO_2, but a somewhat lower content of NaCl and with a slightly higher pH (9·5) than normal in oceanic water. As only 1 ml. is later

added to 300 ml. sea water, the deviations in content of salt and pH in the artificial sea water are of no importance (in both cases, the change produced is less than 1 in the first decimal place).

In the preparation of the artificial sea water a specially constructed vacuum line is used (Figure 1). A glass tube (G) carrying a funnel (T) and stop-cock (H) is inserted in a pyrex glass suction flask (S) through the rubber stopper. A glass vessel (P) is attached to tube (G) by means of a cotton-wool plug. $BaC^{14}O_3$ + a suitable amount of normal $BaCO_3$ to act as a carrier is placed in the vessel (P). A solution of NaOH (generally 5 ml. 0·5N) is placed at the bottom of the suction flask. Then HCl (generally 5 ml. 0·5N) is poured into the funnel. After evacuation the suction flask is closed by a cock immediately outside the side tube (A). The cock (H) is now opened cautiously and the hydrochloric acid is run into vessel (P). This releases CO_2 which diffuses down to the NaOH solution, and is absorbed by it.

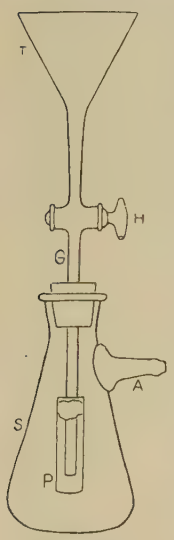

Figure 1. Vacuum line (see text).

During the effervescence in vessel (P), some of the liquid will be thrown on to the cotton-wool, which must eventually be completely steeped in the hydrochloric acid in vessel (P) in order to ensure that the carbon dioxide in the barium carbonate which may have been thrown on to the cotton-wool is released. If the original quantity of hydrochloric acid is not sufficient, a little distilled water is added through the funnel (T).

Figure 2. Glass container.

Although experiments have shown that the total amount of carbon dioxide in the barium carbonate is transferred to the sodium hydroxide solution after 15 minutes, the apparatus is left to stand for a further 60 minutes. After this it is opened and the stopper, together with tubes P and G, funnel (T) and cock (H), is removed. Then 200 ml. glass-distilled water is added. After shaking 10 ml. is removed and titrated electrometrically with hydrochloric acid to pH 9·5. A corresponding amount of hydrochloric acid is added to the remaining 195 ml. and the 10 ml. are poured back. After checking that pH is actually 9·5, a solid rubber stopper is placed in the mouth of the suction flask and the liquid is transferred to 1 ml. glass containers (Figure 2) by means of a graduated (automatic) syringe. The liquid is withdrawn through the side tube (A) of the suction flask after the latter has been turned upside down. The glass containers are then sealed. The relatively high pH (9·5) prevents any appreciable loss of activity during the various manipulations. That this is really so appears from the fact that it was impossible to demonstrate any progressive reduction in activity from the glass container first filled to that last filled. In the later addition of the contents of the glass containers to the water samples in which the photosynthetic activity is to be measured, it is also important that pH should be comparatively high.

For the "Galathea" Expedition glass containers of 4 different strengths were prepared, each containing 1 ml. The different containers, made in series of 200, where each wrapped in appropriately coloured tissue paper. Within series of the same calculated strength the correspondence was fairly close. In later calculations values for the particular series were always used.

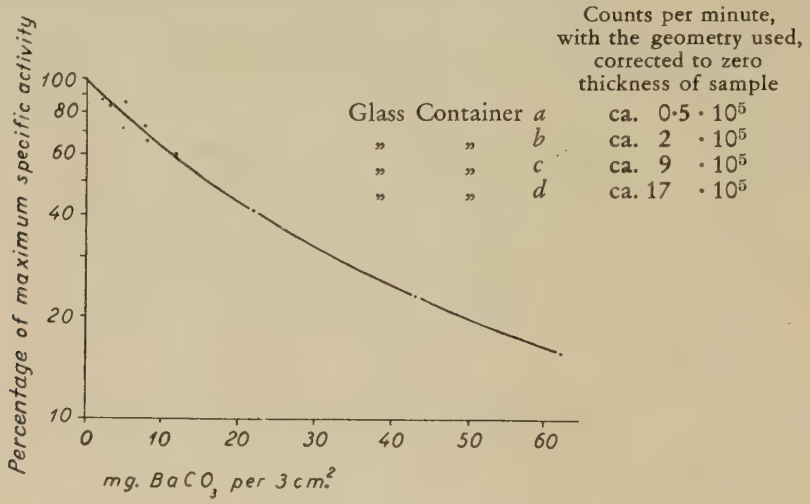

Figure 3. Self-absorption correction curve.

For determining the measurable impulses carbon dioxide was precipitated as barium carbonate, which was then filtered off by the usual collodion filter (3 sq.cm., see p. 123). Carrier was also added. Weight per 3 sq.cm. was always about 20 mg. In the case of containers *a* and *b* 25 µl. was added to 5 ml. water; in the case of containers *c* and *d*, 10 µl. For this Carlsberg micropipettes, checked by weighing, were employed. As the collodion filter changed its weight after a filtration, it was necessary to use a control filter through which only water was filtered. The reason why collodion filters and not ordinary paper filters were used was partly that collodion filters were used in measuring the activity from the algae, partly that paper filters were somewhat unsuitable for the determination of self-absorption, as very small amounts of barium carbonate gave too small activities, presumably because some of the substance entered the body of the filter. This cannot occur with collodion filters. Figure 3 shows a curve made for determining the activity at zero weight.

(b) Determination of the Photosynthetic Activity of Plankton Algae.

After the contents of a C^{14} glass container has been added to a water sample containing plankton algae and exposed to light, part of the C^{14} is found in the organic matter of the plankton algae. If this

quantity of C^{14} is to be used as a measure of the photosynthetic intensity, we must know both the content of total CO_2 in the water and the ratio $\frac{C^{12} + C^{13} + C^{14}}{C^{14}}$ in the total CO_2 of the water. As a rule, however, we shall avoid using the absolute amounts of C^{14}, as only the activity of the experimental water and the activity of the plankton algae are to be determined. If under identical conditions the activity of the experimental water is a, that of the plankton algae b, and the content of total CO_2 in the water c, then the total amount of CO_2 assimilated by the algae is $\frac{b \cdot c}{a}$. This is on the assumption that $C^{14}O_2$ is assimilated at the same rate as $C^{12}O_2$ and that C^{14} is not incorporated in the algae in any other way than through photosynthesis. In Section 3c this question will be discussed in detail.

If pH, titration alkalinity, and temperature are known, it is possible, according to Buch (1945), to determine total CO_2 in fresh water on condition that the titration alkalinity does not approach zero. In sea water it is also necessary to know the content of chloride, which has partly a direct effect, partly an indirect effect through the boric acid, the concentration of which is proportional to the chloride concentration. In oceanic water the calculation of total CO_2 thus becomes slightly more complicated than in fresh water (see Harvey, 1945, pp. 52—73).

If Cl $^0/_{00}$ is known, it is not necessary to determine the titration alkalinity A, as this is equal to 0·000123 Cl $^0/_{00}$ expressed in equiv./l. With brackish water, as with fresh water, it is necessary to determine the titration alkalinity.

As pH varies so little in oceanic surface water, it is unnecessary to determine pH unless very high accuracy is aimed at. If it is put at 8.20, the error in total CO_2 will be 2 to 3 per cent. at most. It will often be sufficient to put total CO_2 at 90 mg./l. with normal oceanic surface water.

The radiation of β-rays by the plankton algae is measured after filtration through a collodion filter (membrane filter from Membranfiltergesellschaft, Göttingen). These filters are kept dry before use. This is a great advantage as compared with the ordinary collodion filters, which must be kept in water. Filtering is done by suction (in the "Galathea" a mechanical pump was used). The filtering surface is 3 sq.cm. Facilities for automatic filling are provided. The filtration device corresponds to that in Calvin *et al.*, 1949, Fig. 40. In the "Galathea" 6 sets of this apparatus were placed so that they could all work at the same time. The filters used nearly resemble the standard filter "mittel" of the factory. 300 ml. distilled water take about 20 minutes to pass through the filter. A considerable quantity of plankton reduces the rate materially; in these circumstances part of the sample is filtered. The maximum size of the pores is 0·5 μ. All marine autotrophic plankton algae are retained. With most — perhaps all — waters it is possible to use filters with a slightly greater pore width (at

most about 1 μ), so that it is possible to increase the rate of filtration materially (see Table 1, p. 128).

When filtration is completed, about 5 ml. sea water free from activity is added for rinsing, etc. Then the filters are placed in special holders (Figure 4), dried in air for about 12 hours, and placed for 20 minutes in a closed container above fuming hydrochloric acid. Experiments have shown that all carbon in inorganic form is removed in this length of time, so that only C^{14} in organic form, which is not destroyed by the process, is left. Immediately afterwards the filters must be dried in a desiccator and if they are not examined at once, kept there. The desiccator must not dry too vigorously. If this is not done, the plankton absorbs water because calcium chloride is developed. Water containing organic matter with dissolved C^{14} may be sucked into the filter. Before the filter is finally dried, it is placed on a special mounting ring and base (C a l v i n *et al.*, 1949, Fig. 41).

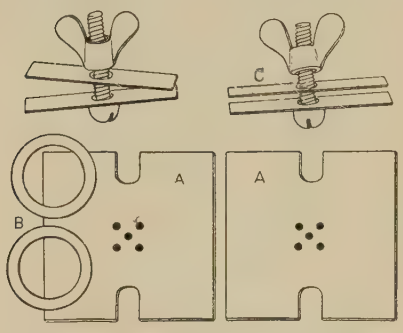

Figure 4. Special holder for collodion filters.

An end-window Geiger-Müller counter tube with a window radius of 7·5 mm. (made by Zerahn and Madsen, Copenhagen) proved most suitable for measurement of the radio-activity. For the "Galathea", counter tubes with a particularly thin window were selected. Care must be taken that the number of impulses is at least 10 times larger than the background, which gives no difficulty so long as a C^{14} glass container of the right strength has been used.

A double counting unit made by Brüel and Kjær, Nærum, Denmark, was used. It has proved robust in all kinds of climate. The technicians of the Expedition were able to correct all faults that developed in the unit without difficulty. A special 220-volt generator, unconnected to other circuits, supplied the current in the "Galathea".

As the geometry in measuring the barium carbonate for determining the activity of the contents of the glass containers is identical with the geometry in measuring the activity of the plankton, the two activities may be directly compared. As the weight of plankton is always below 0·1 mg. per 3 sq.cm., self-absorption in the plankton may be disregarded.

At the start of an experiment, the contents of a glass container are added, by means of an ordinary hypodermic syringe, to the bottle with the sample in which the photosynthesis is to be measured. The container is rinsed with a little water from the sample.

A standard elementary carbon containing C^{14}, mounted on the same mounting ring and base as normal samples and with the same area was always used in addition to normal uranium standards, in order to neutralize the effect of different window thicknesses.

(c) Is the Amount of Organically Bound C^{14} a Measure of the Intensity of Photosynthesis?

If the amount of organically bound C^{14} in the plankton after an experiment is to give an absolute measure of the intensity of photosynthesis (the gross production) the following conditions must be present:— (1) No $C^{14}O_2$ must be incorporated in organic compounds except through photosynthesis, (2) the rate of assimilation of $C^{14}O_2$ must be the same as that of $C^{12}O_2$, (3) no $C^{14}O_2$ must be lost by the respiration which takes place simultaneously with photosynthesis.

None of these conditions are, however, fulfilled absolutely. As is now generally known, both animals and plants assimilate carbon dioxide in the dark. In the plankton algae C^{14} is thus assimilated otherwise than photosynthetically, though the quantities assimilated in this way are very small, as the following experiment illustrates. A glass container was emptied into 1100 ml. of a culture of the green alga *Scenedesmus quadricauda*, from which four 250-ml. bottles fitted with glass stoppers were filled. Two were put in darkness, and two in light (about 15,000 lux). After a period of 105 minutes 100 ml. from each bottle was filtered through collodion filters. The illuminated samples gave an average of 166 counts/min., and the unilluminated, 2 counts/min. The rate of assimilation of carbon dioxide in the dark is thus about 1 per cent. of the rate for photosynthesis in optimum light. In light a little less than 5 per cent. of the total carbon dioxide was assimilated during this experiment. As the amount of C^{14} assimilated apart from photosynthesis is so small, it is an easy matter to correct for this amount.

The error arising from the different rates of assimilation of $C^{14}O_2$ and $C^{12}O_2$ is of a somewhat different order of magnitude. As a result of the process of carboxylation during photosynthesis, isotopes with different masses cannot be expected to react at the same rate (Calvin *et al.*, 1949, p. XII).

Weigl and Calvin (1949) have shown that $C^{12}O_2$ is assimilated faster than $C^{14}O_2$ in barley seedlings, but they do not state how much faster. Their figure, however, seems to suggest about 8 per cent. faster (determined by consumption of total CO_2 and $C^{14}O_2$ during the period of 8 to 20 minutes after illumination began. A respiration intensity simultaneous with photosynthesis corresponding to that in the dark is presupposed. It is also presupposed that no C^{14} is lost during respiration[1]).

According to Urey (1948) it has been demonstrated in Professor Franck's laboratory in Chicago that unicellular algae contain 2·97 per cent. less C^{13} than the carbon dioxide in the nutrient solution.

[1]) In a duplicated paper by Weigl, Warrington, and Calvin, "The Relation of Photosynthesis to Respiration" (1950) it is stated on p. 4 that "The assimilation of $C^{14}O_2$ is about 17 % slower than that of $C^{12}O_2$." It is incomprehensible to me how this value of 17 % is obtained. Assuming that the ratio between C^{12} and C^{14} is the same during respiration as during photosynthesis, there is, even for photosynthesis, an isotope effect of only 4 %.

Assuming that a similar ratio exists between C^{13} and C^{14}, we find that C^{14} is assimilated 6 per cent. more slowly in photosynthesis than C^{12}.

Anderson and Libby (1951) found that the ratio between the C^{14} contents in recent carbonate and recent plant material is $1{\cdot}09 \pm 0{\cdot}03$. On the basis of the factor 1·03 for C^{13}, they are of opinion that we should expect a value of 1·06 for C^{14}. The value found by them is thus in excellent agreement with the theoretical value. From these investigations it is also reasonable to expect that the assimilation of $C^{14}O_2$ during photosynthesis is about 6 per cent. slower than that of $C^{12}O_2$.

A series of experiments was made to decide whether the rate of assimilation of $C^{14}O_2$ actually was 6 per cent. lower. A culture of *Scenedesmus quadricauda* was used for these experiments. The intensity of photosynthesis was determined by measuring the oxygen metabolism (oxygen determined by the Winkler method) and also by means of the C^{14} method. The results showed good agreement. These experiments may not, however, be used for a precise determination of the ratio between the $C^{12}O_2$- and the $C^{14}O_2$-assimilation; the photosynthetic quotient $\frac{O_2\text{-production}}{CO_2\text{-assimilation}}$ is not 1 in *Scenedesmus*, since considerable amounts of fatty substances are produced. Strictly, the photosynthetic quotient is no doubt 1 also in fat-producing organisms. In such cases it is the respiratory quotient which deviates from unity (Rabinowitch, 1945, p. 54). However, for the sake of simplicity this fact is disregarded here. When only carbohydrates are produced by photosynthesis, it is possible to describe the process by the equation $CO_2 + H_2O \rightarrow (CH_2O) + O_2$, but this is not so when fat is also produced.

According to Brown (1948) the basic composition of *Scenedesmus obliquus* — a closely related species — corresponds to the formula $C_6H_{11}O_3$. The apparent photosynthetic equation then can be written:—

$$6\,CO_2 + 5\tfrac{1}{2}\,H_2O \rightarrow C_6H_{11}O_3 + 7\tfrac{1}{4}\,O_2.$$

If we disregard the assimilation of N in the form NO_3^-, the apparent photosynthetic quotient then becomes $\frac{7{\cdot}25}{6} = 1{\cdot}21$. The oxygen method must therefore be assumed to give a 21 per cent. greater yield (in O_2) than the C^{14} method (in CO_2) even if the two carbon isotopes are assimilated at the same rate. If we take it for granted that the ratio of the assimilation of nitrogen in mg. to the assimilation of carbon in mg. is $\frac{1}{16}$ (Harvey, 1945, p. 144), the photosynthetic quotient will be 1·33, as in the culture solution nitrogen was added as nitrate. Thus the oxygen method must be regarded as giving a 33 per cent. greater yield than the C^{14} method.

In a series of experiments made with *Scenedesmus obliquus* on 4. March 1950 (thermostatic water-bath, 20°C., with bottles on a rotat-

ing disk; 15,000 lux; duration of experiment, 3 hours), on the average of 3 parallel experiments with the oxygen method there was a real assimilation of CO_2 (the photosynthetic quotient being put at 1·33) of 0·0248 ± 0·0009 mg. per 100 ml. In two experiments made simultaneously with the C^{14} method a value of 0·0218 ± 0·0010 mg. was obtained. According to these experiments the C^{14} method gives a yield 14 per cent. lower than the oxygen method. The C^{14} method, however, differs from the oxygen method in that it does not give the real assimilation absolutely, as some of the C^{14} assimilated is lost through respiration during the experiment. If we assume that in a 3-hour experiment one third of the total respiration is based on substance produced during the experiment itself, the corrected value for the photosynthesis with the C^{14} method will be 0·0225, since with the oxygen experiments respiration was 9·4 per cent. of the real assimilation. Accordingly $C^{14}O_2$ is assimilated at a rate 9 per cent. lower than that at which $C^{12}O_2$ is assimilated; this may be said to agree very well with the theoretical value 6 per cent.

If, however, an exact experimental demonstration of the isotope effect is desired a method should be used which, like the C^{14} method, measures the carbon dioxide assimilation, not the oxygen production.

As mentioned above, there is a third correction to be made when the value of the real carbon dioxide assimilation is calculated from the C^{14} method. This correction allows for loss of C^{14} through the respiration of matter produced during the experiment itself. In 4-hour experiments this is put at 4 per cent. of the photosynthetic intensity at optimum light intensity. We thus get a total correction of 10 per cent. This convenient figure is used even though there is also a negative correction of about 1 per cent. due to assimilation of C^{14} in the dark, as mentioned at the beginning of this section.

With high light intensities the uncertainty in determining the correction for C^{14}-assimilation apart from photosynthesis and the loss of C^{14} through respiration is thus of very little importance. With very low light intensities, on the other hand, the matter is quite otherwise, as both the assimilation of C^{14} apart from photosynthesis and the loss of C^{14} through respiration become of disproportionately great importance. The C^{14} method is not suitable for the measurement of the intensity of photosynthesis at very low light intensities.

(d) Accuracy of the Measurement of the Photosynthesis in Water Samples.

By choosing glass containers with sufficient C^{14} and counting sufficiently long, it is possible to determine the assimilation of C^{14} with very great precision. Normally the activity is determined to an accuracy of ±5 per cent. To aim at greater accuracy would serve no purpose.

The experiments described in Table 1 were made to discover to what extent the intensity of photosynthesis varies in parallel samples. A large volume of surface water from two tropical localities was thoroughly mixed and distributed among seven to eight 300-ml. bottles. The contents of identical C^{14} glass containers were added to each bottle.

Table 1.

Surface water — Banda Sea		Surface water — Flores Sea	
Time of filtration in minutes for 300 ml.	Activity imp./min.	Time of filtration in minutes for 300 ml.	Activity imp./min.
7	108	7	60
11	115	10	53
36	115	21	48
42	126	40	61
44	110	83	60
45	106	105	56
67	108	109	61
72	117		
	$M = 113 \pm 2$		$M = 57 \pm 2$
	σ (single determination) = 6·1		σ (single determination) = 4·5

After illumination at 18,000 lux for 5 hours, the contents were filtered and the activity of the plankton determined. The variation between samples is greater than the inaccuracy in measuring the activity.

Table 1 also shows the rate of filtration of 300 ml. sea water. As the time of filtration of identical water samples depends on the pore size of the filters and as the coarsest filter had a maximum pore size of just over 1 μ, it is clear that all important autotrophic organisms in the plankton from the samples in question were larger than 1 μ.

4. A Method for Determining the Production of Matter beneath 1 sq.m. Surface of the Sea or a Lake (Method I).

For determining the production of matter under 1 sq.m. of surface, a method resembling G r a n' s oxygen method can be used. Instead of measuring oxygen metabolism, the intensity of photosynthesis is determined by the C^{14} method.

With an all-glass water-bottle (see A a b y e J e n s e n and S t e e m a n n N i e l s e n, 1952) 500 ml. water is taken from the various layers of water in which photosynthesis is believed to take place. This may be decided by measuring the penetration of light into the sea (see p. 133). After a 300-ml. bottle (pyrex, with glass stoppers) has been filled and the contents of a C^{14} container added, the bottle is lowered to the depth from which the sample came. This is done either immediately before sunrise or when the sun is at its meridian altitude. The bottle is raised again, either in the first case when the sun is at its meridian altitude, or in the second case immediately after sunset. In both cases, the photosynthesis measured relates to half a day, and the value found has only to be multiplied by 2 to relate it to the whole day. Then a factor is applied to the values for the various depths to give the total photosynthesis under 1 sq.m. surface of the sea.

Figure 5 (broken line) shows the measurements made in the northernmost part of the Benguela Current, off Loanda in Angola (West Africa). It is clear that production of organic matter is highest at a

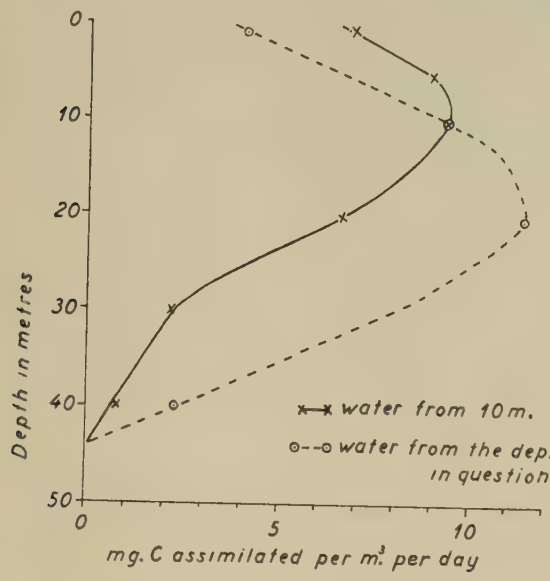

Figure 5. Curves showing the production of organic matter in the Benguela Current, off Loanda.

depth of 20 m. Close to the surface the light intensity is so great that the photosynthetic intensity is reduced. Below the depth of 20 m. the light intensity is too low. It appears from the full-drawn curve, which shows the photosynthesis at the various depths when water from a depth of 10 m. is used at all depths, that the characteristic form of the curve is not entirely due to different amounts of plankton at the various depths. In principle the broken curve has the same form as the full-drawn curve. In this case, however, the amount of plankton is greater farther down than at a depth of 10 m., as appears from the fact that the full-drawn curve clearly lies to the left of the broken curve at depths greater than 10 m. The production of matter (the gross production) in this experiment was determined as 335 mg. assimilated C per sq.m. of surface.

The experiment was carried out on a bright day. The influence of a more or less overcast sky on experiments of this kind was discussed in Steemann Nielsen (1951) pp. 31—34 (see further below, p. 133).

In addition to the real carbon dioxide assimilation of the phytoplankton (the gross production), the respiration of the total number of organisms in the experimental bottles is determined by Gran's oxygen method. The apparent assimilation (the net production) of the phytoplankton is not, however, obtained by subtracting this quantity from the real assimilation. The phytoplankton's own respiration is often only a fraction of the total respiration, as the respiration of bacteria, other heterotrophic plants, and minor zooplankton organisms is often relatively great. If the net production of the phytoplankton is to be determined from the gross production, the value for total respiration

should not be used; net production should rather be calculated theoretically. According to S t e m a n n N i e l s e n (1951, p. 37) net production in Danish waters is on an average 75 per cent. of gross production.

By the C^{14} method, in which no value for any respiration is determined, net production must be calculated theoretically from the gross production. For the tropics a net production of 75 per cent. seems very reasonable from theoretical considerations. However, since it is gross production which is measured, this quantity should always be stated.

The method of suspending bottles is particularly suitable for investigations near land, but on an expedition like the "Galathea" it is too time-consuming. A station takes at least 6 hours and keeping the ship stationary for so long costs a lot of money, particularly with a relatively large vessel. To enable a considerable number of stations to be occupied on the "Galathea" Expedition, it was therefore essential to use another modification of the C^{14} method.

5. A Second Method for Determining the Production of Matter beneath 1 sq.m. Surface of the Sea or a Lake (Method II).

With this method, water samples from the various depths, after addition of C^{14} are exposed to a definite light intensity in a water-bath at the same temperature as the sea. After 3 to 4 hours the plankton is filtered off and the photosynthetic intensity determined in the usual way. From the value of the photosynthetic intensity found for a given light intensity and temperature, the production of matter by photosynthesis through 24 hours can be calculated if we know firstly the dependence of photosynthesis on the light intensity, and secondly the light intensity at various times of the day at the depths from which the samples originate.

On account of the ship's movement at sea, the water-bath (for detailed description, see A a b y e J e n s e n and S t e e m a n n N i e l s e n, in preparation) is kept tightly closed. Through a trap-door in the middle of the top cover the bottles can easily be placed on the rotating disk in the middle of the bath, which can accomodate nine 300-ml. bottles. The spindle on which the disk rotates passes through the wall of the water-bath to a motor supplying the motive power. The whole front wall is glass, so that the experimental bottles can be illuminated by the twelve 20-W. tubular fluorescent lamps (Philips 33a) which give a light with a spectral composition near that of daylight. A mirror is placed behind the lamps.

Before the start of an experiment the temperature of the water in the water-bath is adjusted, by adding ice, to about 1°C. below the temperature wanted. During a 4-hour experiment the temperature increases by 2°C. The increase in temperature is slight partly because the water-bath is very effectively insulated, and partly because tubular fluorescent lamps are used, which radiate very little heat. On that side

of the water-bath facing the source of light partial insulation is provided by an extra pane of glass placed 1 cm. outside the pane in the bath.

All parts of the water-bath, including the rotating disk, are treated with silver-bronze, the light intensity thus being increased by about 50 per cent. With new fluorescent lamps the effective light intensity illuminating the water in the experimental bottles is about 20,000 international lux. This intensity, however, falls to about 18,000 lux in a comparatively short time. After a burning period of about 500 hours the light intensity is 14,000 lux: the lamps should be replaced before that stage is reached.

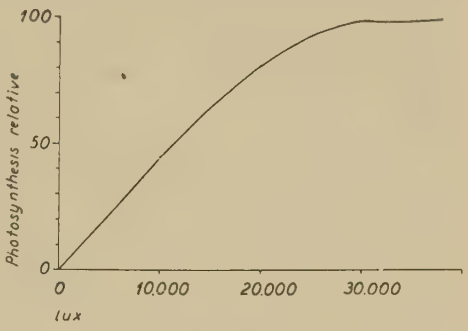

Figure 6. Relation between light intensity and rate of photosynthesis in tropical surface plankton.

Maximum photosynthesis is obtained at different light intensities according to the origin of the plankton. Four different series of experiments indicate that the maximum photosynthesis of tropical plankton from the surface is obtained at about 30,000 international lux (see Figure 6). At 20,000 lux (with quite new lamps) photosynthesis is 20 per cent. less than the maximum, at 18,000 lux 25 per cent., and at 14,000 lux 38 per cent. Different conditions obtain for plankton from deeper layers in the tropics. The experiments with this plankton have not yet been concluded, but it can be stated that maximum photosynthesis occurs at lower intensities of light than with the surface plankton. In the case of surface plankton from temperate zones the light intensity producing maximum photosynthesis is also lower than in the tropics; for autumn plankton from Danish waters this is about 7,000 lux (S t e e m a n n N i e l s e n, 1937).

It is presumably undesirable to use higher intensities than 20,000 lux on the water-bath, since otherwise with plankton from deeper layers the light intensity might be too high to produce maximum photosynthesis. The fact that in the water-bath maximum photosynthesis is obtained for plankton from deeper layers, but not for surface plankton, is of no practical importance in calculating the photosynthesis in the various water-layers from the water-bath experiments. With plankton from deeper layers photosynthesis proceeds at low light intensities only. The fact that the rate of photosynthesis is at maximum at different light intensities with surface and subsurface plankton is due to the presence of different amounts of one or more of the enzymes involved in photosynthesis. This has no effect on the intensity of photosynthesis at low light intensities. If a light intensity is used which generates a photosynthesis 70 to 80 per cent. lower that the maximum in the surface

plankton, the observed values for the photosynthesis of the surface and subsurface plankton can be compared more directly.

As mentioned at the beginning of this section, it is possible to calculate the production of matter per surface unit per 24 hours provided that (1) the photosynthetic intensity of the plankton at a given light intensity, (2) the dependence of photosynthesis on the light intensity (in the form of a relative curve), and finally (3) the light intensity at the various depths at various times of day are known. As the calculation was found to involve a great deal of work, a simpler — and probably better — method was used instead. The first method of calculation was used only for checking.

For this simpler method it is only necessary to know the penetration of light into the sea and the photosynthetic intensity at a given light intensity for water samples from three different depths, namely, the surface, one at which the blue and green light is about 10 per cent. of that at the surface, and one at which it is about 1 per cent.

The following formula was derived from observations at four "Galathea" stations in the tropics, where simultaneous measurements were made with bottles suspended in the sea and placed in the thermostatic water-bath:—

$$\text{Production of matter per sq.m. per 24 hours} = \frac{(2a+2b+c)\cdot d\cdot e}{5\cdot 2}\ \text{mg. C}$$

where a is the photosynthesis in mg. C per hour per cu. m. at 18,000 lux in surface water,

b is that in water from a depth with 10 per cent. of the surface light,

and c that in water from a depth with 1 per cent. of the surface light;

d is the depth in m. at which the light is 1 per cent. of the total quantity of blue and green light at the surface;

and e is the number of hours from sunrise to sunset.

If the light intensity at which a, b, and c are observed differs slightly from 18,000 lux, a correction obtained from the curve in Figure 6 should be applied.

The formula rests primarily on the fact that, taking all the experiments into account, photosynthesis in bright weather in the tropics at the optimum depth in the sea (10 m. in the experiment illustrated in Figure 5) from sunrise to sunset corresponds to about 75 per cent. of the maximum photosynthesis (water from the upper layers of water) at optimum light over an equal period. In the second place, all experiments show that when the same kind of water is suspended at all depths, the total photosynthesis under 1 sq.m. of surface is equal to the assimilation value at the optimum depth (measured per cu.m.) multiplied by half the depth of the photosynthetic zone measured in m. (see Figure 5). The photosynthetic layer reaches to the depth at which 1 per cent. of the total blue and green light is found. As the photosynthesis in the deepest layers of the photosynthetic zone has no great

quantitative importance, the value for photosynthesis at 18,000 lux in the water from the depth with 1 per cent. of the light is entered in the formula at half its value.

It should be emphasized that the formula only applies to the tropics. In higher latitudes the formula is slightly different. In the case of the tropics it appears to be possible to determine the production of matter per surface unit by this method with an accuracy of at least ±20 per cent., which should normally be quite sufficient. Greater accuracy may be obtained by taking samples from more depths than the three mentioned above.

The production of matter in the sea of course depends on weather conditions, although to a less degree than would be expected at first sight. This question will be discussed in detail in a later publication (but see Steemann Nielsen, 1951, pp. 31—34). Only two factors will be mentioned here. In the first place a reduction of the surface light by an overcast sky normally results in an increase in the production of matter in the upper water-layers. In summer in the temperate and frigid zones and at all seasons in the tropics the amount of light in bright weather is too strong in the upper layers of water (see Figure 5). Secondly when the surface light is reduced, the total thickness of the water-layers in which production of matter takes place does not decrease to the same extent. If the light intensity at the surface is a, and at a depth b is $\frac{a}{100}$, when the light at the surface is reduced to $\frac{a}{2}$, the light intensity $\frac{a}{100}$ occurs at the depth $\frac{b \times 85}{100}$. If, correspondingly, it falls to the intensity $\frac{a}{3}$ or $\frac{a}{10}$, the intensity $\frac{a}{100}$ occurs at the depths $\frac{b \times 77}{100}$ and $\frac{b \times 50}{100}$. Accordingly, even when the sky is so overcast that the light at the surface is reduced to $\frac{1}{10}$ of the normal, the depth of the water-layer in which production of matter takes place has fallen by only one-half.

There are presumably few localities in the tropics in which an overcast sky may be expected to produce a diminution of the production of matter by more than about 20 per cent. of the average. In order to correct for weather conditions all values calculated for the production per area are reduced by 10 per cent.

The penetration of light into the sea is observed by a submarine photometer, used in conjunction with a deck photometer. In the "Galathea" investigations an apparatus was used similar to that used by Steemann Nielsen (1951), details of which will be given in a later publication.

In a wind, the "Galathea" gathered leeway very quickly, on account of the very high superstructure. As a result routine measurements could not be made farther down than about 50 m., and for greater depths it was necessary to extrapolate. The following light filters (Chance

Optical Glass) were used: O R 1 (red), O Gr 1 (green), and O B 10 (blue). In addition one or two neutral filters (either O N 31, O N 10, or both) were usually placed in front of the colour filter.

6. Riley's Experiments on the Production of Matter in the Sea.

As mentioned in the introduction, the American marine biologist R i l e y (1938, 1939, 1941a, 1941b) carried out a number of investigations in which he used a special modification of G r a n' s oxygen method for determining the production of matter by the plankton; some of these experiments were made in the Sargasso Sea. As R i l e y' s figures have been used for estimating the total production of matter in the seas (see, for instance, R a b i n o w i t c h, 1945), and as the "Galathea" Expedition obtained such very different figures for production in tropical seas by the C^{14} method, it is expedient to subject R i l e y' s investigations to a detailed analysis. I shall mainly discuss the 1939 paper, in which the investigations from the Sargasso Sea were published.

R i l e y describes the method as follows (p. 146):— "The experiments were conducted in the following way: 250-ml. bottles were filled with surface water in the same way as for routine oxygen tests. The bottles were exposed for a period of three days. When the vessel was in port, the bottles were hung over the side at a depth of one meter in a position where they would receive direct sunlight all day. At sea it was necessary to adopt a makeshift procedure in which the bottles were suspended in a tub on deck, and the water in the tub, surrounding the bottles, was changed frequently in order to maintain a normal temperature."

The experiment was continued for three days in order to obtain a sufficient effect, and in the Tortugas region the experiment covered a period of seven days[1]). In passing it may be remarked that S t e e m a n n N i e l s e n (1932) has shown that this kind of experiment should not be extended beyond one day, as otherwise very essential changes take place which affect the intensity of both photosynthesis and respiration.

Since in R i l e y' s experiments some of the bottles were black, and since also the oxygen was determined at the start of the experiment, it was possible to determine both oxygen consumption and oxygen production, of which the latter should be an expression of the photosynthesis. R i l e y (1938) mentions three different sources of error in the method which, in his opinion, all cause the observed values of the photosynthesis to be smaller than the real ones. He writes (p. 341) "The only conclusion that can be drawn at present in regard to this difference is that the experiments give a minimal estimate of photosynthesis."

[1]) R i l e y and G o r g y (1948) repeated the experiments at sixteen stations in the Sargasso Sea. The experiments then lasted 24 hours. It was, however, not possible to measure the rate of photosynthesis, since oxygen changes were not significantly different from zero.

For the five stations in the Sargasso Sea 3513—3520 Riley (1939) found an average oxygen consumption of 0·11 (0·04—0·17) mg. O_2 per day and an oxygen production of 0·07 (0·03—0·16) mg. O_2 per day. The ratio of production to consumption was 0·64 (0·5—1·0) on the average. The quotient in this is quite improbable for natural conditions in the sea, where an order of magnitude of at least 3 is to be expected (see Steemann Nielsen, 1951, p. 36). Riley is himself aware that the value for oxygen consumption in the bottles is much greater than in nature, as he refers to the increase of the oxygen consumption in sea water enclosed in bottles; this has been pointed out from many quarters. Whereas in nature a fairly large amount of organic matter exists in sea water at all depths and localities which is not attacked by bacteria, it will be attacked as soon as the water is enclosed in a bottle, presumably as result of the surfaces present. According to Waksman and Renn (1936) a quantity of oxygen of 0·12—0·51 mg./l. is easily consumed in three days, as shown by Riley in the Sargasso Sea. While there can be no doubt that the large oxygen consumption is due to respiration of bacteria when the water is in the bottle, a different state of affairs exists as regards oxygen production, as measured by the difference between the oxygen content of transparent and black bottles. Riley takes it for granted that this difference is due to the photosynthetic activity of the phytoplankton, but this can hardly be the case.

We may compare the Sargasso Sea with the tropical western part of the Indian Ocean, where the plankton is at least as abundant as that in the Sargasso Sea, and if anything a little more so.

In measurements of the rate of photosynthesis in surface water (0·5 m.) from six stations (265—274; see Figure 7, p. 136) situated on a line between 3°30′S., 50°20′E. to 2°04′S., 64°00′E., an average carbon assimilation of 0·15 mg. per hour per cu.m. at 18,000 lux was found by the "Galathea" Expedition. If, as in the case of Riley's experiments, the samples had been placed in full sunlight at the surface for a whole day, we should have found a daily C-assimilation of $\frac{0{\cdot}15 \times 12 \times 60}{100} =$ 1·08 mg. per cu.m. = 0·00108 mg. per litre. According to Riley, in the Sargasso Sea an average of $\frac{0{\cdot}07 \times 12}{32} = 0{\cdot}026$ mg. C was assimilated per litre per day. Thus on the average the rate found for the Indian Ocean is only 4 per cent. of what Riley estimated for the Sargasso Sea. It can hardly have been the intensity of photosynthesis which Riley measured by subtracting the oxygen content in the black bottles from that in the transparent bottles. But what, then, did he demonstrate? Apparently it was simply the bactericidal effect of the sunlight. It is a well known fact that sunlight is highly capable of killing bacteria. Not only are the ultra-violet rays active, and they are by far the most active, but the visible light is also effective. For example, according to Meader, McCulloch (1945) states that *Staphylococcus aureus* is killed by direct sunlight in an hour in the

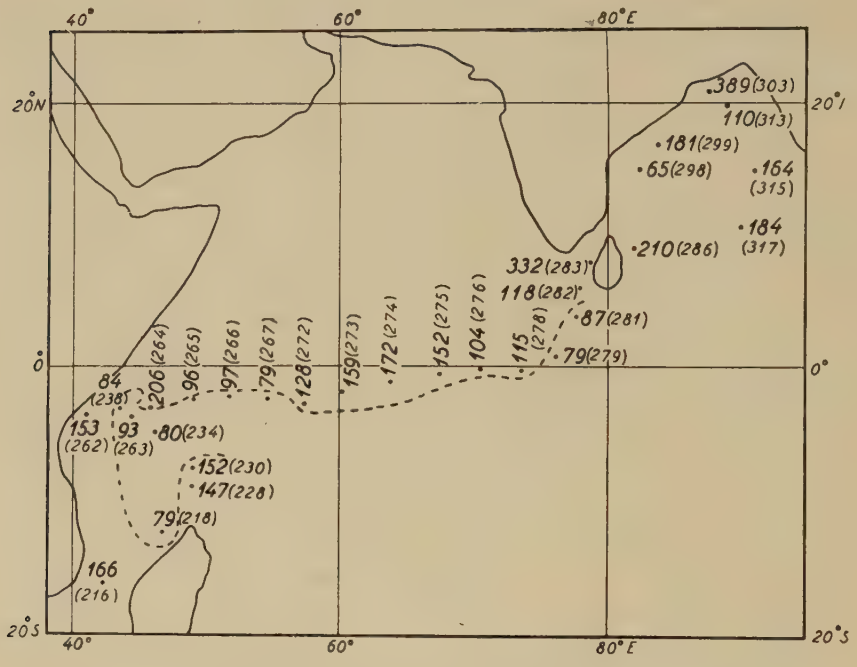

Figure 7. Production of matter (mg. C per sq. m. per day) on a section across the Indian Ocean. Station numbers in brackets.

middle of the day, whereas if the same sunlight first passes through a glass plate of 8 mm., 4½ hours are required. Even though the bacteria in Riley's light experiments were protected by the glass of the bottles and to a less degree also by the layer of water above the bottles, they would still have been exposed to the deadly effect of the light rays. It is therefore quite natural that the consumption of oxygen in the transparent bottles should have been lower than that in the black.

The order of magnitude of the production of matter by phytoplankton in oligotrophic tropical areas is very different from that stated by Riley in 1939. As an average for all tropical stations Riley reckons that 530 g. carbon is fixed in the phytoplankton per year. A comparison with similar areas investigated by the "Galathea" Expedition gives reason to expect that the correct order of magnitude is about 40 g. C. Riley's values for the production of matter as calculated per surface unit are at least 10 times too high.

As opposed to the data for oligotrophic waters those for eutrophic waters (experiments lasting 24 hours) are of course reliable. Riley (1941) thus makes an important contribution to the estimation of productivity on a eutrophic coastal bank.

7. The Production of Matter on a Section across the Indian Ocean.

The "Galathea" Expedition visited all the great oceans, and large numbers of observations were made of the production of matter and also of the variation in photosynthetic intensity with depth. As an example of these investigations data from a section across the Indian Ocean near the Equator are given in Figure 7. The estimated production of matter in mg. C assimilated per day per sq.m. is recorded against the station numbers. The section is not discussed here in detail, as this requires a discussion of a great number of other physical and chemical data. The whole of the material will of course be published in later papers.

Although the original data from the section across the Indian Ocean at the preparation of this article still were onboard the "Galathea" cruising in the Pacific, it was intended provisionally to give the results from this section. Unfortunately a systematic error has been introduced. All values for the production of matter given in Figure 7 are 30 percent to low. The estimation of the production of matter in the hydrosphere as a whole given on p. 138 is, however, based on the revised data.

8. Production of Matter in the Hydrosphere as a Whole.

It was mentioned in the introduction that using Riley's and Seiwell's figures together with a few others Rabinowitch (1945) attempted to calculate the total production of matter in all the sea areas of the earth. Starting from an average net production of 375 g. C assimilated per sq.m. per year and a total sea area of 361×10^6 sq.km., he arrived at a total carbon fixation of $15{\cdot}5 \times 10^{10}$ tons C per year[1]). This amount is nearly 10 times as large as that given by Schroeder (1919) for the land.

As shown above, the order of magnitude of Riley's and Seiwell's figures is not correct and consequently Rabinowitch's calculations are not correct either.

In contrast to Riley's assumption that the production of matter in different parts of the sea was much the same, the "Galathea" Expedition's measurements show that the previous conception of the tropical parts of the oceans as generally poor in production of matter is in better agreement with fact. On the whole we must expect considerable variations from region to region. This undoubtedly makes it more difficult to obtain an idea of the total production of matter in the seas, and investigations on a much greater scale than a single circumnavigation of the globe are needed to get absolutely reliable figures for the production of matter in the seas.

According to the "Galathea" Expedition's data an average annual gross production of matter of 55 g. assimilated carbon per sq.m. seems

[1]) According to Riley (1944) the total oceanic metabolism is $12{\cdot}6 \pm 8{\cdot}2 \times 10^{10}$ tons carbon per year.

probable. If we reckon on a 25 per cent. loss through respiration (Rabinowitch's figure, 15 per cent., is too small) and a sea area of 361×10^6 sq.km., we obtain a total net production per year in the sea of $1{\cdot}5 \times 10^{10}$ tons carbon. This is slightly less than the $1{\cdot}6 \times 10^{10}$ tons which Schroeder (1919) estimates as produced on land.

For man, therefore, the sea will hardly ever have the same importance as the land as a source of nutrition. Direct utilization of the plankton algae is probably out of the question, in view of their small size and the low concentrations in which they occur in the sea. When the organic matter is eaten by man in the form of fish, there are normally several links between the plankton algae and the fish. As, for each link, we must reckon a loss of about 90 per cent. of the organic matter, it is evident that only a fairly small part of the organic matter produced in the sea can be consumed by man. Nevertheless there is no reason to despise the sea's contribution to man's nutrition. If the population of the earth continues to increase, it will be necessary to consume an increasingly large part of the plant material direct, and the fish in the sea will play a more and more predominant role as suppliers of protein. Moreover, it should be possible to intensify the fisheries in most parts of the world. Investigation of the production of matter can give valuable information on local possibilities of large-scale fishing.

9. Summary.

A method for measuring the photosynthesis of plankton algae in a water sample by means of assimilated C^{14} is described. It is shown that the assimilation of C^{14} in organic matter otherwise than by photosynthesis is of quite insignificant importance. An account is given of the isotope effect in photosynthesis.

Two different methods for the measurement of production of matter per surface unit are described. In the first method samples of water are taken from the various depths and transferred to bottles with glass stoppers. After addition of C^{14}, the bottles are suspended at the depths from which the samples were taken, and left there from noon to sunset, for instance.

In the other method the bottles are placed in a water-bath which is illuminated by a definite light intensity. The penetration of light in the sea is determined at the same time. The production of matter per surface unit is calculated by means of a formula involving the determination of the depth at which 1 per cent. of the total amount of green and blue light occurs, and measurement of the intensities of assimilation in the water-bath. The formula, which applies to the tropics, has been derived by comparing the results from all tropical stations, at which observations by the two methods were made simultaneously.

The values found for production of matter on a section across the Indian Ocean are recorded. The net production of matter for all sea regions on the globe is estimated at about $1{\cdot}5 \times 10^{10}$ tons of carbon per year, which is slightly less than the amount produced on land, and the

hitherto accepted figures for the production of matter in the sea have proved to be greatly exaggerated.

The Carlsberg Foundation has made valuable grants towards the performance of the present work, for which I offer my respectful thanks. Miss Hilde Levi, Ph. D., of the Zoophysiological Laboratory in Copenhagen, besides teaching me the technique of tracer studies, has assisted me in many ways in working out the methods, for which I offer my cordial thanks.

Finally, I am greatly obliged to A. F. Bruun, Ph. D., leader of the "Galathea" Expedition, and the Committee of the Expedition for facilities on board, and not least to E. Aabye Jensen, Civil Engineer, who assisted in working out the methods and, after the writer's return home from the expedition, conscientiously carried out all the experiments on board.

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Condition of Stocks of Halibut in the Pacific.

By

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THERE are many fisheries which must have begun when man first used a hook or a net. But there were few really great fisheries until power became available. Steam expanded the fishing grounds and the markets of Europe; it also led to the building of the transcontinental railroads that opened the western states of America and gave them access to their own great eastern markets. It brought industrialization and highly organized systems of food preservation and distribution to both the United States and Europe. All this came to the Pacific halibut fisheries about as soon as it came to those of Europe and since then the stocks of fish in the American Pacific have felt the impact of each technological improvement as soon as those of the North Sea. As a result, in all that concerns the intensity of fishing and its effects, the Pacific halibut fishery is as old as that of Europe.

Of the two, the history of the Pacific fishery is much more easily followed. People of European stock settled America and they demanded familiar fish. For many years a ready market existed for halibut, but not for the many strange fish that were taken with it. The fishery became a specialized long-line one, depending on halibut alone for success or failure. The fleets have been correspondingly sensitive to the distribution and abundance of these halibut stocks, and of them alone, at least until the regulations of recent years and the growth of supplementary fisheries such as those for tuna.

The records of this simple, uncomplicated fishery were good. They were useful in navigation and were required by insurance and government agencies. They were necessary guides from past experience as to season and yield, where and when fishing was to be done. They were kept by a homogeneous, intelligent body of men. Their scientific value was recognized and collection was begun in 1916, early enough to

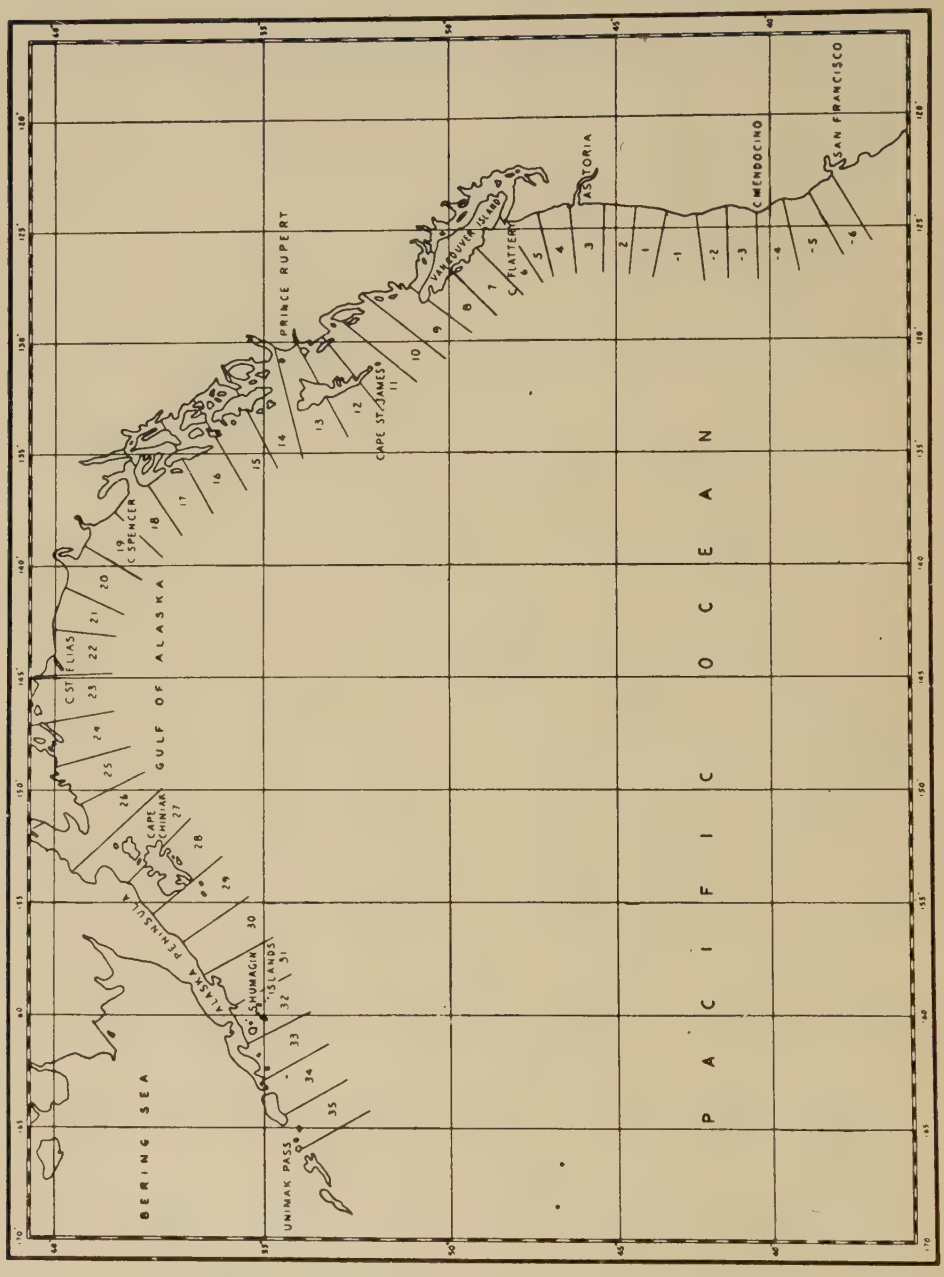

Figure 1. Pacific coast of America north of 35° N. Latitude, showing the statistical areas as defined by the International Fisheries Commission.

Thompson and Van Cleve. Life history of the Pacific halibut. (IFC No. 9, 1936, p. 37, Fig. 8).

obtain even some of the first records of fishing on virgin stocks. Since 1924 the form of these voluntary records has been perpetuated and made obligatory by the regulations of the International Fisheries Commission of the United States and Canada.

The result is what I believe to be one of the most complete and least complicated records of any fishery. It is remarkable how sensitive the record is, warranting precision in its treatment.

These statistics have been analysed in a series of reports, first by the British Columbia Fisheries Department and then, after the signing of a treaty between Canada and the United States in 1924, by the International Fisheries Commission. So much was determined in the course of the investigation, and thereafter taken for granted in those reports, that it has become necessary to review the evidence bearing on the several points which have aroused discussion.

These points are the dominance of the fishery in determining the condition of the stocks and the nature of the criteria which distinguish natural from fishery-caused fluctuations in those stocks. In dealing with these points it is necessary to lay emphasis upon the most fundamental fact of all — that within all population changes is found the waxing and waning of an accumulated stock according to the mortality rate, in accord with the well known laws applicable to all living things, including man.

It has often been said that the halibut regulation presents the only definite case of sustained improvement of an overfished deep-sea fishery. This, I believe, is true and the fact should lend special importance to the principles which have been deliberately used to obtain this improvement.

Two main categories of facts are available, as for any fishery. The log of each vessel shows the catch in pounds and the number of sets of units of gear to make this catch. For the categories of place and time desired, the catches and numbers of sets are summed. From this the catch per unit is obtained. Since a certain percentage of the records for any category are not usable for one reason or another, it is necessary to weight the number of sets used to represent the whole fleet. On the western grounds, for example, B e l l states that as high as 80 per cent. of the fleet provides good records and the percentage is more than 50 for all areas, despite the most critical treatment.

Statistics were collected and have been compiled according to a system of 60-mile long divisions of the coast, from California to the Bering Sea. Such linear divisions were feasible because the continental slopes, and consequently the halibut banks, form a long narrow coastwise strip 2500 miles in length. This is an ideal arrangement for differentiation of the effects of biological and economic factors that vary with latitude or distance. The coast forms the abscissa of a huge graph (Figure 1).

Analysis has shown that for statistical and regulatory purposes it is advisable to distinguish two main areas, differing by age of the fishery,

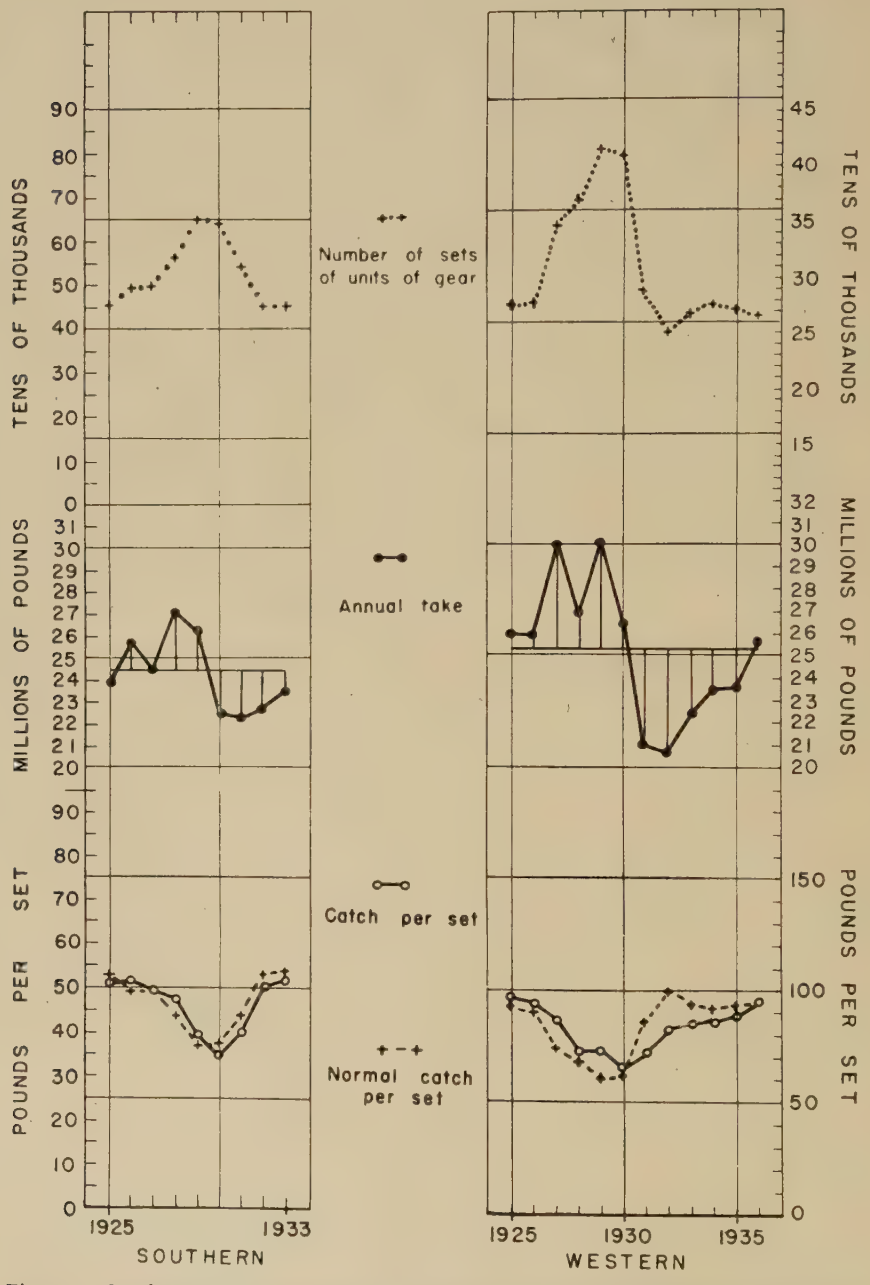

Figure 2. Southern and western grounds. Statistics of landings, number of sets of gear, and catch per set. 1925 to 1933 in southern and 1925 to 1936 in western. The catch per set is compared to that which would have occurred had the take been the constant shown for each period, when it is the "normal" shown.

Adapted: Thompson. Effect of Fishing on Stocks of Halibut in the Pacific. 1950, pp. 7 and 8, Figs. 1 and 2.

type of vessel in the fleet, and stage of exploitation, as well as by the characteristic migrations of sections of the stocks. The two meet in linear division 18. The fishery began first in the southern area, more adjacent to the landing ports. It has been carried on there by a fleet of boats more numerous and smaller than those necessary for the long voyage west. Due to the intensity of the fishery and the longer period of exploitation, the southern area came to have a stock largely of immatures because they were allowed a shorter life and were fished to a lower level of abundance. The western stocks have had for a long time a much larger proportion of matures.

The matures migrate rather freely in contrast to the immatures, as shown by extensive tagging. While western mature fish do move within their own area, they rarely enter that to the south. As a result the southern area has for a long time consisted actually of a series of semi-isolated stocks of predominantly young fish drifting only slowly from one bank to those adjacent.

These stocks owe their homogeneity and statistical integration to the similarity of the factors acting upon them, especially in the past to the active, sensitive fishery that has probed incessantly to take advantage of every shade of difference in abundance from bank to bank or spot to spot.

In both areas the records are better and more complete since 1925 when the International Fisheries Commission began to collect them under the authority of the treaty between the United States and Canada.

Because of its longer history, the greater volume of its early records, and the more extensive changes in the stocks, the southern area gives the more diagramatic picture of what happened and the reader may profitably study it first.

A short period, from 1925 to 1933, in this area is selected for discussion first since it is desirable to focus attention on short-term variations as a basis for the understanding of those of a longer term. The period chosen, moreover, includes both decline and increase in amount of fishing in annual catch and in catch per unit. It includes the year of first effective regulation of catch (Figure 2, left).

In this period and district, the values of catch per unit and number of units have approached a reciprocal or inverse relationship, such as they would have had if the annual total take had been constant. This has not been completely constant, of course, but the greatest variation of the annual catch from the mean in this nine-year period is only 11 per cent. It is the same as for the 23-year period ending in 1947 (Figure 3).

To show graphically how much of the variability in the catch per unit can be thus accounted for, the actual values of the catch per unit (unbroken line) are plotted along with the values they would have had (broken line), had the annual catch been constant. These latter hypothetical values are then the reciprocals of the number of units, assuming the constant necessary for the reciprocal to be equal to the mean of the

annual catches for the period. This true reciprocal[1]) or inverse relationship, it should be carefully noted, is used for comparison with the actual data. It shows how closely the actual data approach this relationship, but in itself does not indicate which variable is the independent one, or cause.

It is interesting to see that this close correspondence extends over the whole period from 1925 to 1947. Whatever is true of the relationship between variables for the short period seems to apply to the longer (Figures 3 and 4).

This behaviour of the catch per unit is of the utmost importance because it represents the magnitude of the stock of fish. This stock has, then, tended to vary inversely as the number of sets of a unit of gear; that is, there was an approach to a reciprocal relationship between the two variables (Figures 5 and 6), their product approximating a constant.

As a first step in analysis, it is vital to know which of the two near-reciprocal variables was the independent one, because if it was the

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[1]) That is, as c and f, when $c = \frac{C}{f}$. Using this terminology: $c_r = \frac{C_r}{f_r}$, when C_r is the actual variable annual total catch; c_r, the catch per set of a unit of gear; and f_r, the number of sets in any given year, r. And $c_n = \frac{C_n}{f_r}$, when C_n is a constant, and c_n, the catch per unit, calculated from this constant.

In the sense in which the term reciprocal relationship is used in the paper, c_n and f_r are reciprocals; but c_r and f_r are not although they approach such a relationship in so far as C_r approaches constancy.

It is possible to make a quantitative statement of this approach by calculating a coefficient of correlation between c_r and f_r. A true reciprocal relationship between the number of units and the catch per unit based on a constant, C_n, or any other constant would give a correlation coefficient of —1·00 for the logarithm of the two variables, because by definition their product must be equal to the constant. The coefficient thus calculated for 23 years, from 1925 on, is —·96. The difference between —1·00 and —·96 is simply a mathematical expression of the *effect of the deviations from constancy of the annual catches*, whatever their cause and it has no significance as an expression of causal relationship. Decision as to that must come from other evidence. If the reader does not approve of this use of the correlation coefficient, he is, of course, free to disregard it, as the calculation does not change the facts.

The statement, $\frac{\text{Total catch of any year}}{\text{Catch per set}}$ or $\frac{C_r}{c_r} = f_r$, number of sets, is bound to be true, however extreme the changes in total catch. After 1931, the annual take was limited by law, but these limits to the total annual catches varied in both periods. Before 1931 they were set by economic factors above the constant value, C_n, used here as a basis for comparison. After 1931 they were set below this constant. While set above, a continuous decline in stocks occurred. When set below, this decline ceased and an increase began. As long as these limits set by economics or by law exceeded the constant, C_n, their deviations from that value produced declines in stock and vice versa. The decline and increase was correlated, not with the mere existence of a limit or limits, but with the value of this limit. As will be pointed out in the text, the deviations of annual total catch determined the timing, the direction, and the rate of change in stocks.

If the reader wishes to explore the changes in the fishery prior to 1925, he is referred to Thompson, 1950, pages 55 to 60.

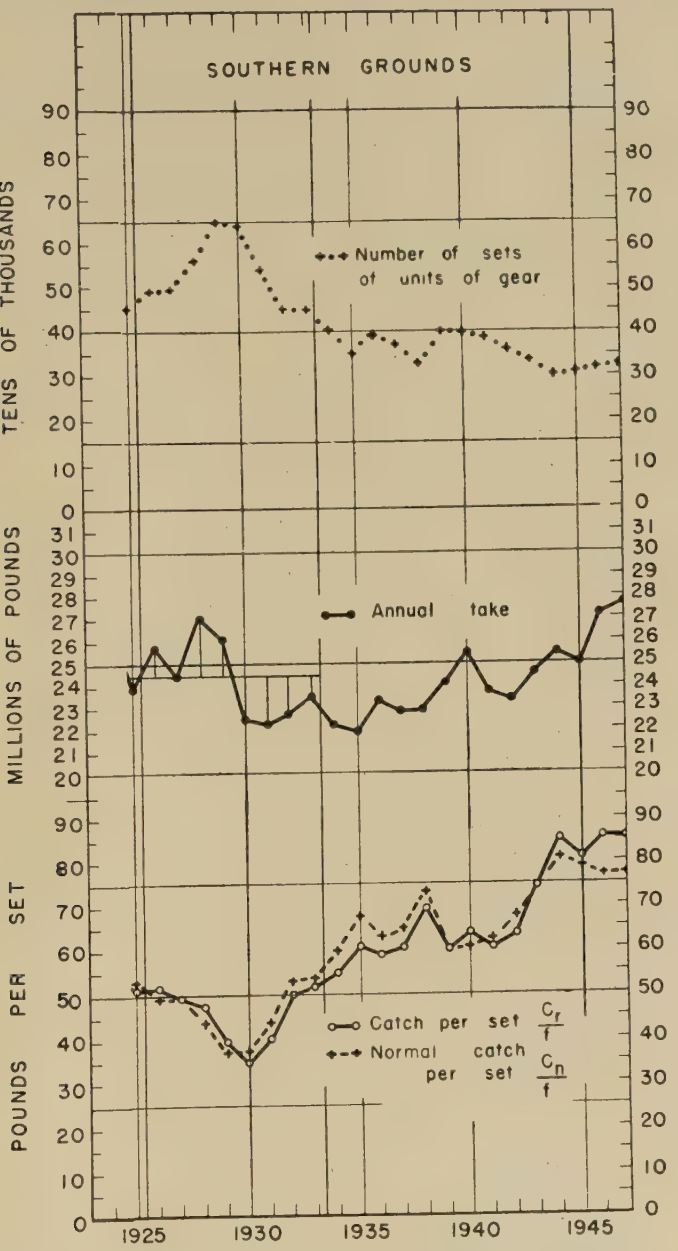

Figure 3. Southern grounds. Statistics of landings, number of sets of gear, and catch per set, 1925 to 1947. Normal catch per set is the normal take, here the hypothetical constant, divided by number of sets of gear.

Adapted: Thompson. Effect of Fishing on Stocks of Halibut in the Pacific. 1950, p. 8, Fig. 2.

fishery there was little room left for natural fluctuations in stock or productivity.

From a practical viewpoint there is a presumption that the fishery was the independent variable. The halibut fishery has to a large extent always been a "spot" fishery, reducing abundance to a minimum fixed by costs of operation wherever a temporary increase showed. Log book records have been full of references to such spots, each known by its own precise navigational bearings. The history of each such spot has been in miniature that of the whole coast. The first sets gave a heavy yield and each successive day's fishing gave less until it was no longer more profitable there than elsewhere. The discovery of such spots certainly did not reduce fishing activity. It increased and was accompanied by a sharp decrease in abundance despite initial heavy yield. When left alone, the stock on the spot recuperated and after some time the fishermen would return to test the spot again.

My own first experience on the halibut banks was a trip to such a spot, and the subsequent growth of my own knowledge of the banks was largely in terms of spots and their history. Years afterward it was by good fortune that a tagging experiment was carried on during the exploitation of one in Nichols Bay. The return of tags was initially very heavy, rapidly decreased, but finally reached a very high percentage with temporary suspension of the fishery there.

When the statistics for the whole of the southern district, as well as the western, are examined, the same sequence of events can be seen (see Figure 2, page 144). For the period 1925 to 1933 the statistics are good. Referring to the data from the southern district, in the first part of this period, 1925 to 1931, the annual take was in excess of the average for the whole period as will be seen from the graph. As in the case of the individual spot, the *excess annual catches* came from an *increased fishery* and accompanied a *falling abundance*, as shown by the catch per unit. During the second part of the period, from 1931 to 1933, the annual catches were *reduced* with a *decreased fishery* and they accompanied a *rising abundance*. The trends were reversed. That too corresponded to what happened on the spot after it was left to recuperate. As on the spot so on the banks as a whole, the time of change from excess to reduced catches was that of the change from a falling to a rising abundance. The same sequence was observed even more plainly on the western grounds between 1925 and 1936.

The fact that *larger* catches accompanied *falling* abundance and vice versa is a vital point. It is an effect that would result from the presence of an accumulation; it would not follow a natural change.

The reaction of the stock of fish is very plainly that of an accumulation. It resembles that of any reservoir in a flowing system which has an inflow or increment, and an outflow or removal. As in a reservoir, removal at a greater rate than inflow means reduction in the accumulation. Removal at a lesser rate means increase in the accumulation. Every water system in our cities shows the same.

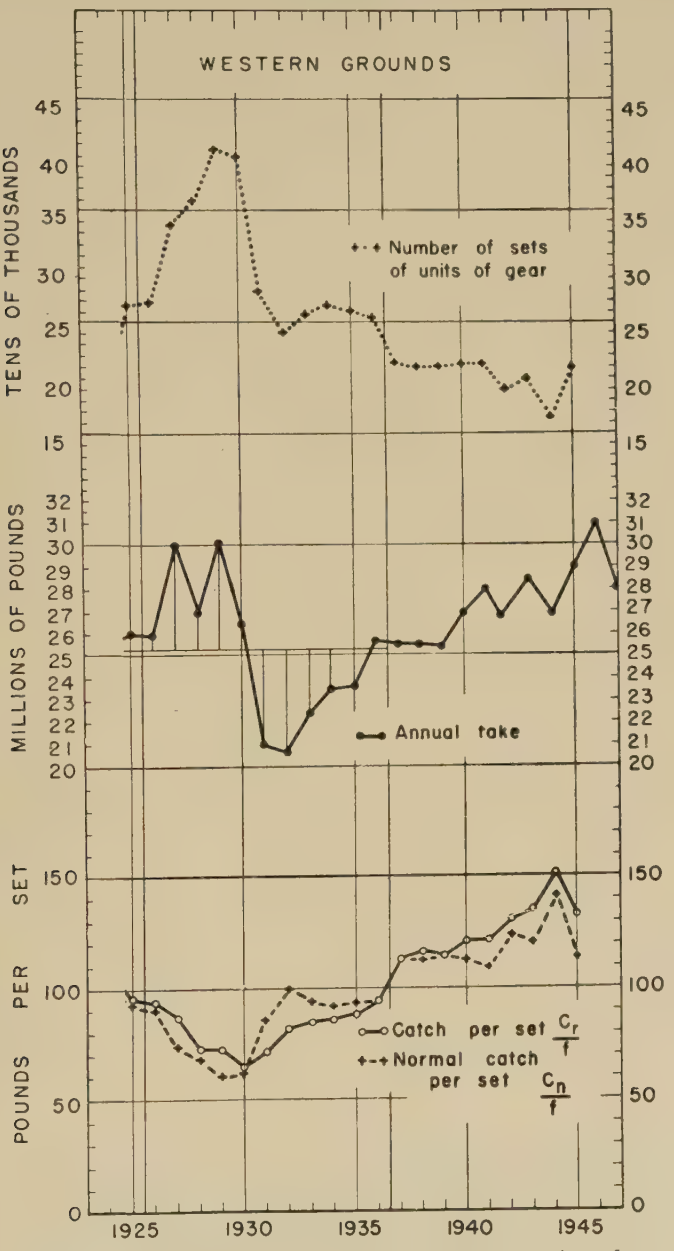

Figure 4. Western grounds. Statistics of landings, number of sets of gear, and catch per set, 1925 to 1947. Normal catch per set is the normal take, here the hypothetical constant, divided by number of sets of gear.

Adapted: Thompson. Effect of Fishing on Stocks of Halibut in the Pacific. 1950, p. 7, Fig. 1.

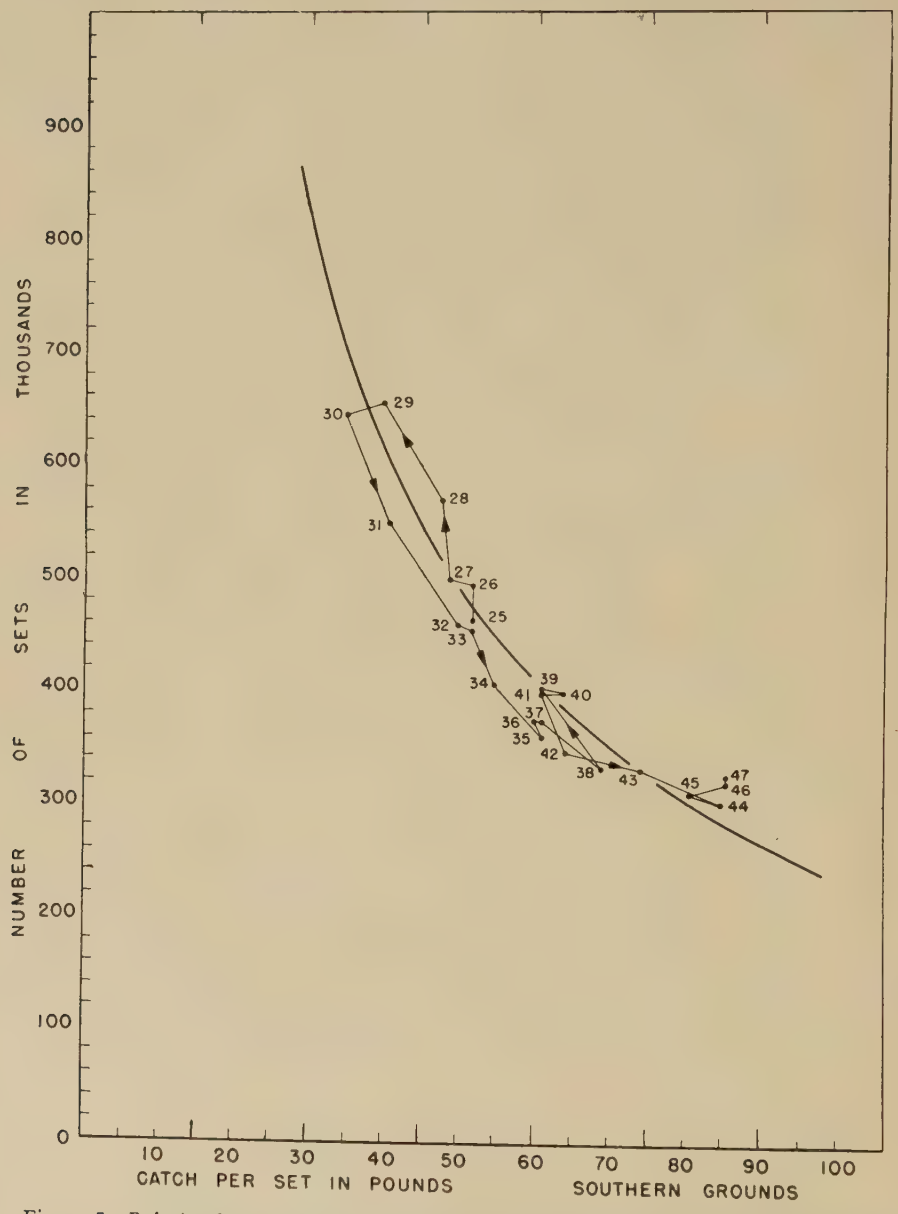

Figure 5. Relationship of number of sets of gear and catch per set on the southern grounds from 1925 to 1947. The time sequence is shown by arrows. The line of constant product, 24,429,739 pounds, is shown.

Thompson. Effect of Fishing on Stocks of Halibut in the Pacific. 1950, p. 12, Fig. 4.

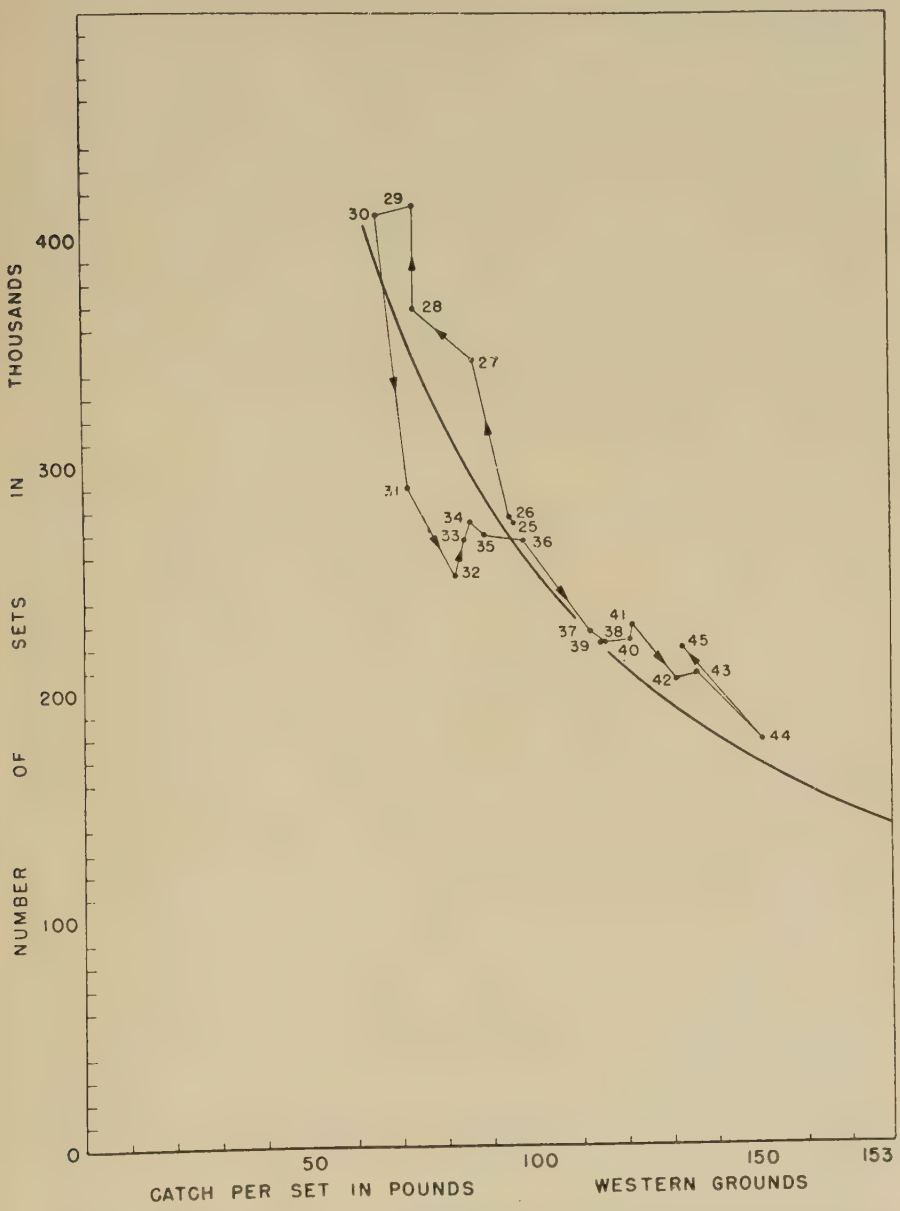

Figure 6. Relationship of number of sets of gear and catch per set on the western grounds from 1925 to 1945. The time sequence is shown by arrows. The line of constant product, 25,169,116 pounds, is shown.

Thompson. Effect of Fishing on Stocks of Halibut in the Pacific. 1950, p. 11, Fig. 3.

The presence of such an accumulation, or reservoir of living organisms, is one of the most fundamental and best proved of all scientific facts regarding our fisheries. Every study of age- or size-groups of fish since the time of Petersen has proved the existence of this reservoir, in the form of survivors of successive age-groups. That they are *age*-groups is just another way of saying that the accumulation has an annual increment. That this increment is removed in time is equally undeniable. The direct evidence from halibut statistics, as to the rise and fall of this living reservoir of fish with the varying balance between increment and removal, is simply in accord with proved fact. A statistical model of such a reservoir, conforming to all essential facts regarding this accumulation and the effects of the fishery upon it, can be readily set up. This has been done by Thompson and Bell (Figures 7, 8, 9, and 10) and in a simplified form by Thompson (Figures 11 and 12). (See also Figure 5, page 150, and Figure 6, page 151). The result corresponds to the actual.

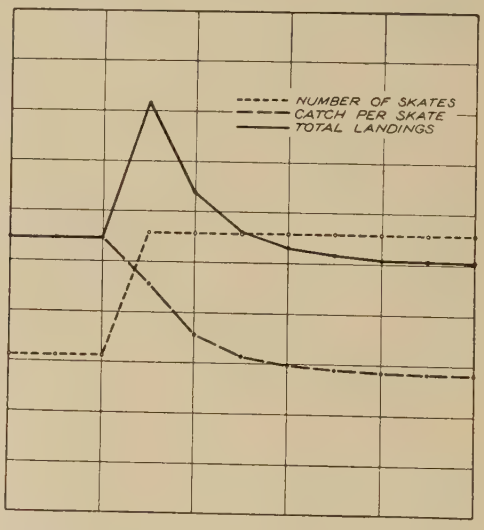

Figure 7. Statistical model showing effect of change of intensity or fishing mortality from 40 % to 60 % with a 10 % natural mortality in each case upon landings and catch per skate.
Thompson and Bell. Biological statistics of the Pacific halibut fishery. (2) (IFC No. 8, 1934, p. 37, Fig. 10).

The model shown in Figure 7 illustrates the behaviour of the reservoir after a single sustained increase in the fishery; that in Figure 11, the behaviour during an increase followed by a decrease in the fishery. The first conforms to what happened repeatedly during the pre-regulation period; the latter to what happened in the period 1925 to 1931. It would be a remarkable coincidence to have the actual events, if due to natural causes, conform so closely to the same model structure, particularly in the coincidence of excess removals and declines in stocks.

There is, in the behaviour of this reservoir, a means of distinguishing the effect of the fishery from the effect of natural factors. Such a criterion is badly needed because it is a prevalent practice to allege natural factors as an indefinite but all-embracing explanation of any fluctuation.

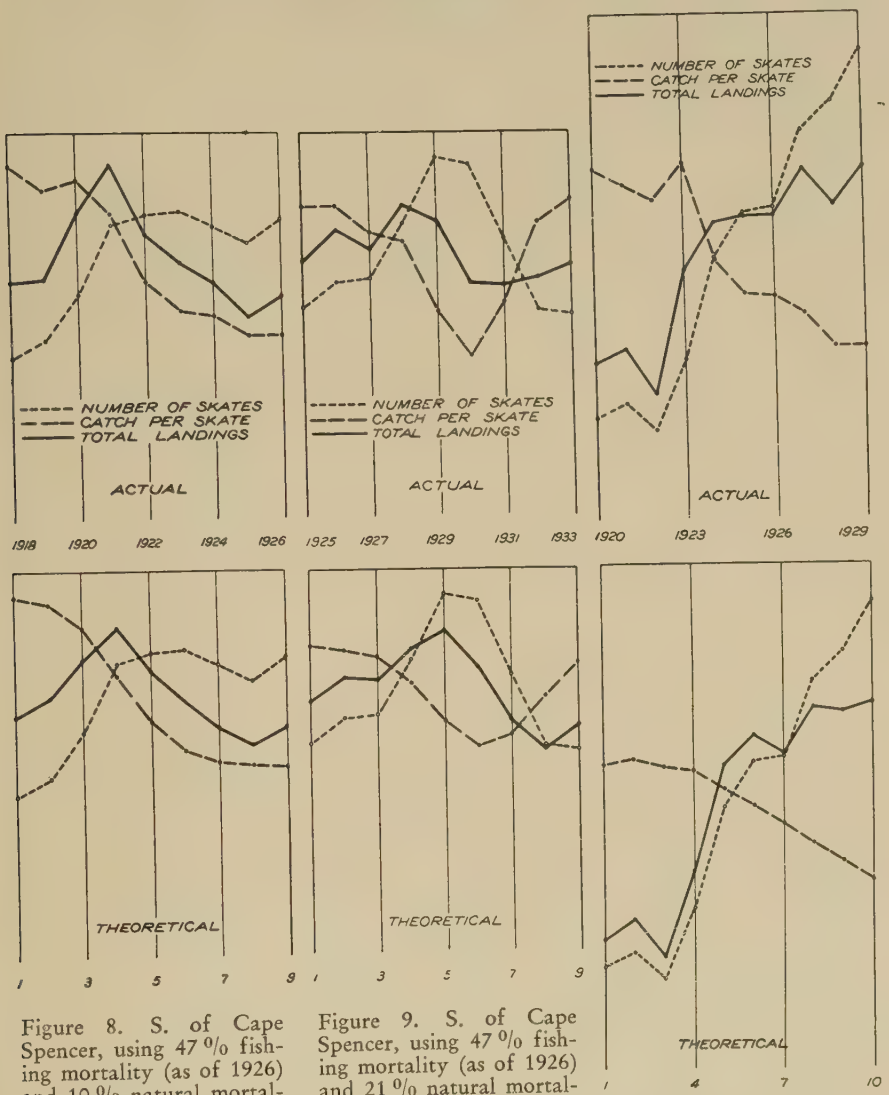

Figure 8. S. of Cape Spencer, using 47 % fishing mortality (as of 1926) and 10 % natural mortality, 1918 to 1926.
(p. 41, Fig. 12.)

Figure 9. S. of Cape Spencer, using 47 % fishing mortality (as of 1926) and 21 % natural mortality (as of 1926).
(p. 43, Fig. 14.)

Figure 10. W. of Cape Spencer, using 12 % fishing mortality (as of 1926) and 20 % natural mortality, 1920 to 1929.
(p. 46, Fig. 17.)

Actual and theoretical catch per skate, total landings, and number of skates fished on grounds south and west of Cape Spencer.

Thompson and Bell. Biological statistics of the Pacific halibut fishery. (2) (IFC No. 8, 1934.)

Here, in all these instances in statistical models and in actual data, the *excess* removals at the hands of an *increased* fishery is plainly shown. The excess goes to the fishery. It has not gone to some unseen natural mortality. The level of abundance has fallen. The timing of

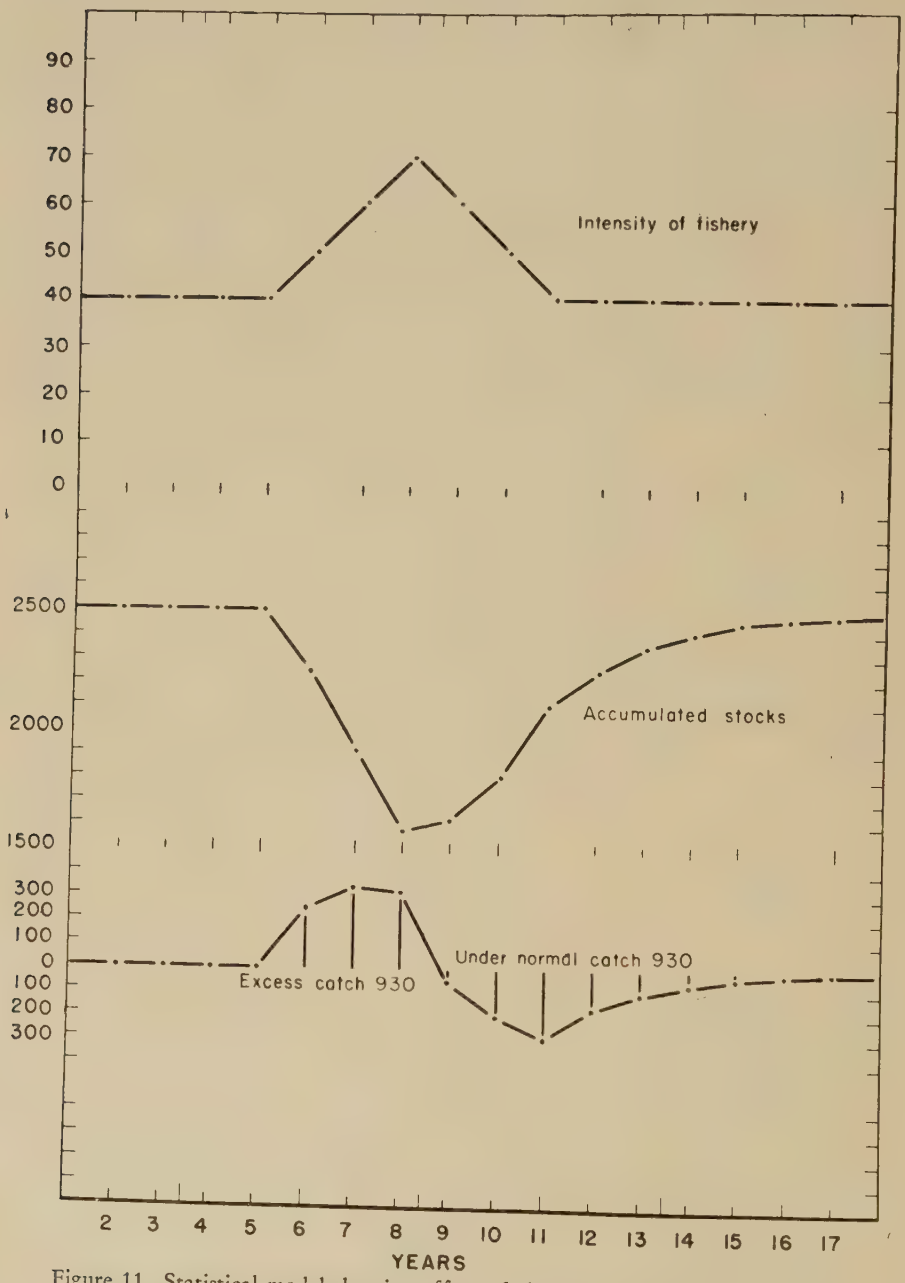

Figure 11. Statistical model showing effect of changing intensity on the stocks. (See also Figure 12.)

Thompson. Effect of Fishing on Stocks of Halibut in the Pacific. 1950, p. 25, Fig. 7.

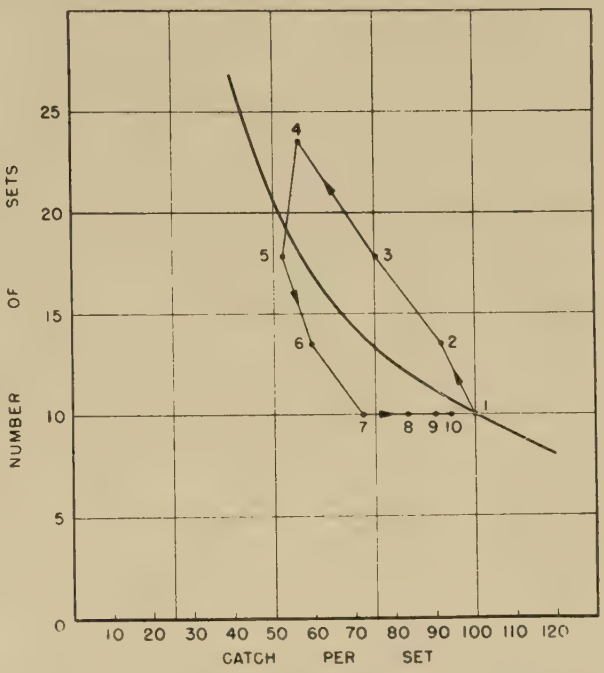

Figure 12. Theoretical case showing relationship of number of sets of gear and catch per set during a temporary increase of fishing intensity. The time sequence is shown by arrows. The line along which the points would have fallen, if the product of the two had been a constant equal to the annual increment, is shown, as an illustration of a reciprocal relationship modified by the buffer action of an accumulated stock.

Thompson. Effect of Fishing on Stocks of Halibut in the Pacific. 1950, p. 13, Fig. 5.

the sequence is in itself proof of cause and effect. It is as plain as though you yourself stood at a tap draining a container, opened the tap, and filled a cup held in your own hand; and at the same time observed the fall in level of liquid in the container.

There might still be some doubt in your mind that someone else, unknown to you, had opened a tap labelled "natural factors" and had been the real cause of the decline of the level in the container. It would be comforting to both the fisherman and to the scientist without data, but groping for a cause, to take refuge in such an all-inclusive explanation. But a little experimenting would soon satisfy you if each time you opened the tap the level changed at the instant of opening. So the same sequence is seen in the fishery on the southern grounds where heavy annual catches began periods of decrease in the accumulated stock. This occurred in three distinct steps — 1910 to 1919, 1920 to 1925, and 1925 to 1931. Each is followed by a levelling-out of yield. The sequence is the same and the timing of the changes corresponds. The three steps added together make the total decline in accumulated stock (Figure 13).

The fishery took its excess catch by an increase in the number of units fished, as you can see from any of the graphs which we have presented[1]). This increase in the number of units fished was an actual

[1]) The increased removal in the form of annual catches is, of course, the significant factor in changing the population of fish however or wherever those annual catches were taken. The increase in gear fished is incidental and is mainly of interest in determining the causal factor and its characteristics.

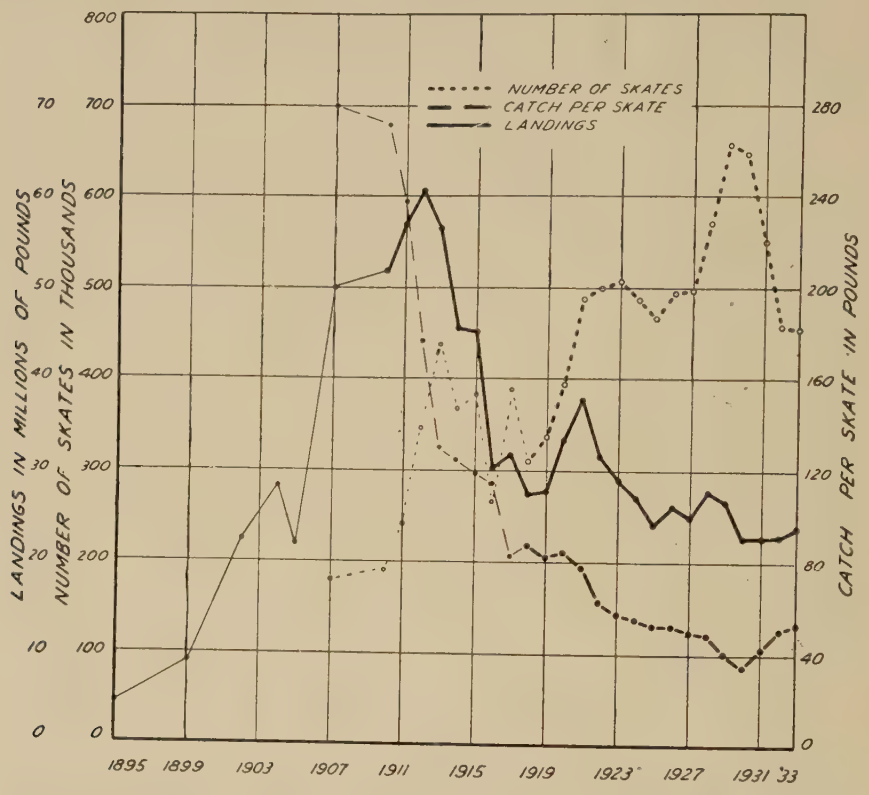

Figure 13. Landings, catch per 6-line skate in pounds, and number of skates fished on grounds south of Cape Spencer. The lighter lines indicate less complete records. Thompson and Bell. Biological statistics of the Pacific halibut fishery. (2) (IFC No. 8, 1934, p. 13, Fig. 2).

increase in the fishing fleet. It should be remembered that prior to 1931 this fleet was unregulated and economically free. It was fishing at full efficiency as far as prevailing economic conditions would permit and to the limits of its capacity without regulation. It had no large unused reserve of men and gear. Increasing the fleet meant construction and financing extending over a period at least two or three years in advance, hence in advance of each decline in stock. It was usually construction of new types of boats. The decline in stock could not have caused the simultaneous, in fact prior, increase in the fleet, by any conceivable reasoning. There can be absolutely no question as to which variable in the reciprocal relationship is the independent one — it is the number of sets of fishing gear.

There is, moreover, a regularity about these three steps which merits attention because it departs from the irregularity of natural processes (see Figure 13 above). The proportionately great excess catch in the first step produced a great reduction in abundance. A medium excess in the second step produced a medium fall in abundance and the

Figure 14. Landings, catch per 6-line skate, and number of skates fished on grounds west of Cape Spencer.

Thompson and Bell. Biological statistics of the Pacific halibut fishery. (2) (IFC No. 8, 1934, p. 14, Fig. 3).

small excess in the last produced the smallest actual decrease. The comparison I can make is only a visual one. To my eye, the progression in the magnitude of change in the annual catches and in the abundance argues a decrease in the relative importance of the accumulation and a closer dependence on the greater constancy of the annual accretion.

It is not possible to escape the conclusion that the fishery is the independent variable in these changes. They are built up of the successive reduction of individual area or spot fisheries to a level determined by the costs of operation. The excess removals that reduce the accumulation pass through the catches and are not lost in the ocean. Had natural factors dominated, the catch and abundance would have risen together. Not once did that happen. Whatever reductions nature might have made are overwhelmed. Certainly they do not determine the levels reached.

Had the fishery not been the determinant, its unregulated catches should not have reduced the abundance to an economic minimum and no shift of the fishery would have been necessary. Then all the demand

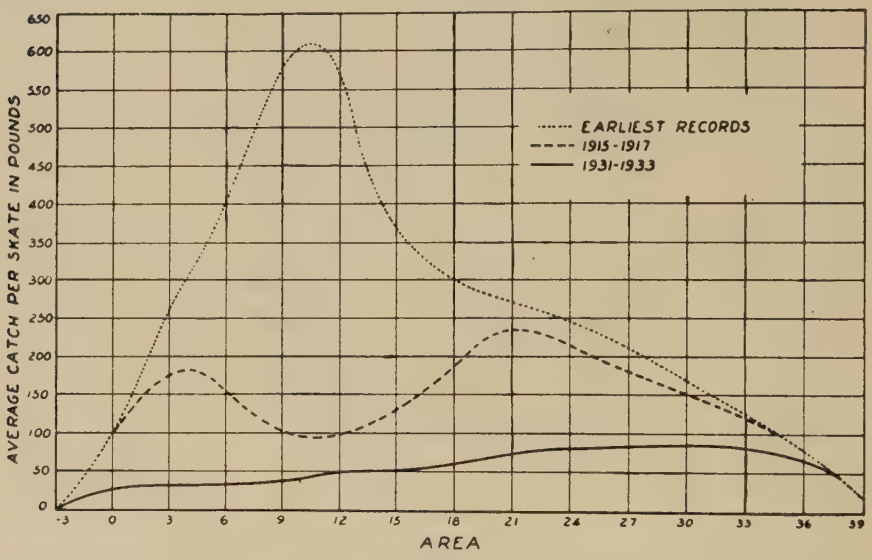

Figure 15. The distribution of abundance of halibut along the Pacific coast of America as indicated by the average catch per skate in each area (see Figure 7). The approximate original distribution of abundance is shown by the earliest records, and subsequent changes due to fishing are indicated by the later records.

Thompson and Van Cleve. Life history of the Pacific halibut. (IFC No. 9. 1936, p. 38, Fig. 9).

of the markets should have been satisfied from the nearby banks. This is completely at variance with the facts. No possible reconstruction of the history of the shift to the westward can be fitted into any reasonable theory of the dominant effect of natural factors (Figure 14).

The reduction in accumulated stock on the banks occurred on all parts of the banks but at different times and rates. Thompson and Van Cleve give a graphic picture of this reduction (Figure 15). The degree to which it has occurred is a function of the amount of fishing[1]). It replaced a natural distribution of abundance along the coast with one dependent upon the cost of operations as reflecting the distance from the markets, hence an abundance which increased to the north and west along the coast. Successive reports of the International Fisheries Commission have called attention to this and to the dominant part played by the fishery.

The evenness, or lack of great variability from bank to bank as distinct from the trend of the increase of distribution of abundance with distance westward, is very significant in the light it throws on the

[1]) At this point it is pertinent to call attention to the fact that the volume of an accumulation with a constant inflow varies inversely as the rate of removal. This is the same as the relationship between the catch per unit which varies inversely as the number of units, the latter determining the rate of removal. Hence the catch per unit can be inverse to the number of units fished and at the same time represent the magnitude of the accumulation or average stock as the fisherman sees it (Thompson, 1950, p. 45).

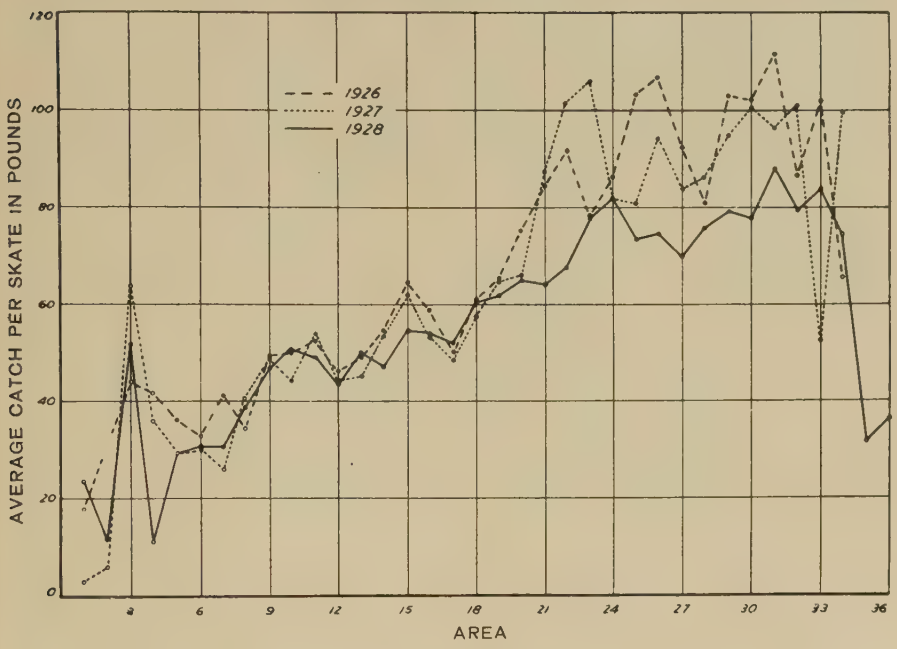

Figure 16. Average weights caught per 6-line skate-set in 1926, 1927, and 1928 for all areas.

Thompson, Dunlop, and Bell. Biological statistics of the Pacific halibut fishery. (IFC No. 6, 1931, p. 66, Fig. 24).

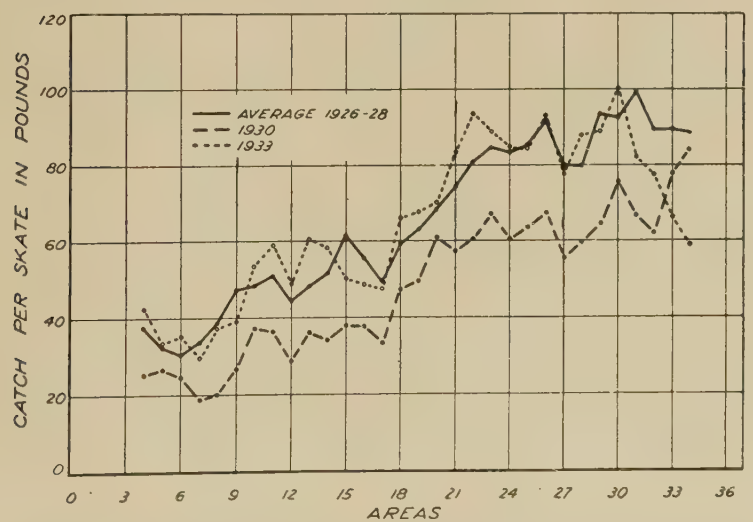

Figure 17. Catch per 6-line skate in pounds by 60-mile sections of the coast from Willapa Harbor (4) to Sanak Island (34). Cape Spencer is in Area 18.

ibid. (2) (IFC No. 8. 1934, p. 17, Fig. 6).

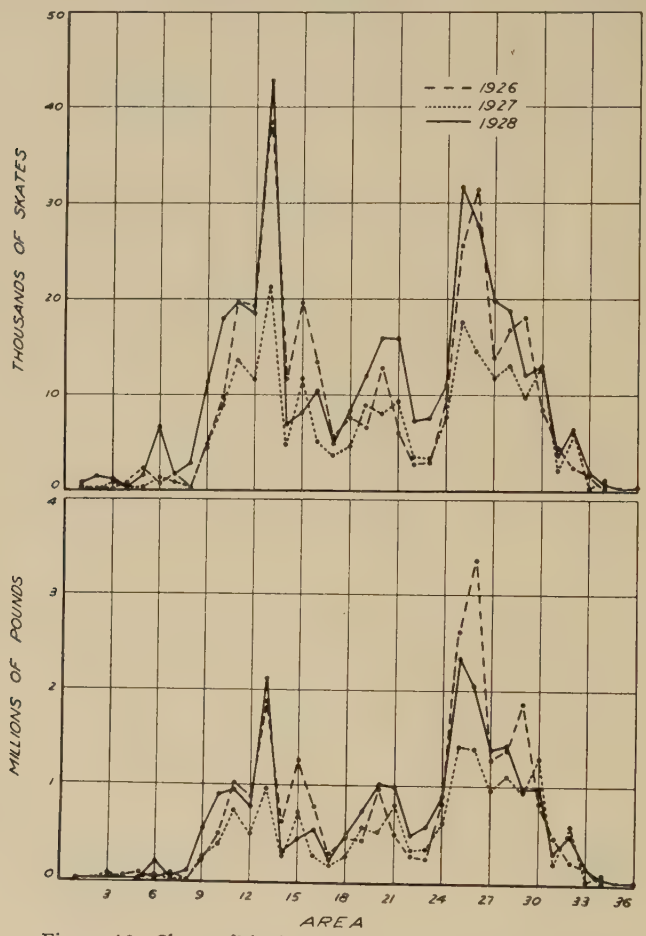

Figure 18. Skates fished and total weight caught in 1926, 1927, and 1928, both United States and Canadian, by vessels furnishing log records.

Thompson, Dunlop, and Bell. Biological statistics of the Pacific halibut fishery. (IFC No. 6, 1931, p. 70, Fig. 26).

relative effect of fishing and of natural factors (Figures 16 and 17). In Report No. 1 of the International Fisheries Commission, page 14:

"... A relative abundance exists on the more distant banks, with a marked degree of depletion on the nearer, the degree of depletion being dependent upon the distance of the banks from the markets..."

(See also Thompson, Dunlop, and Bell, 1931, pp. 67 and 68.)

The evidence is clear that very different amounts of fishing and annual catch in different areas have been required to maintain this evenly graduated economic minimum level of abundance (Figure 18). The yield and the amount of fishing from certain areas is very much greater than in others, even though the fishery obtains only the prevailing economic minimum catch per unit in each. The implication is, of

course, that in some areas the stock is much larger and more productive than in others, not in density but in area covered. The areas available for halibut vary widely and inspection of the grounds will show this.

The fishery, to so distribute itself, is necessarily sensitive to small differences in profit of operation. This is rapidly reduced on the less extensive banks and the fleet shifts accordingly. If this level happens to rise because of natural or other causes, it must be that it is promptly reduced by concentration of the fleet; if it happens to fall below the prevailing levels, it must be that it is relieved of the pressure of fishing and promptly revives. The whole process ends in a balanced distribution of effort which results in an evenly graduated yield per unit of effort but not in an even distribution of total catch.

It is, of course, very improbable that nature would produce such an even gradation of abundance either on the banks as a whole or on adjacent banks. Nature did not do so when the fishery began. It is improbable, if it should so happen once, that it should happen year after year, as it does, in accord with economic factors not conceivably closely correlated with the environment of the halibut. So the graduated level of abundance is maintained regardless of natural factors.

Yet, as we have seen, differences in total productivity, as distinct from the level of abundance shown by the yield per unit, do arise among the sections of the banks. It is then conceivable that natural changes in the productivity of the banks as a whole could arise without disturbing the level of abundance, as set by economic factors, and that this productivity would show in greater annual yields. Yet, as we have seen, this annual productivity tends toward constancy and when it varies from this constancy its variations behave in the manner of excess or under withdrawals from an accumulated stock. The effects they produce are those of withdrawals which are more or less than the income of a reservoir set in a dynamic system — a reservoir of life flowing through successive ages of the stock.

Since it is definitely known that an accumulation of stock occurs, it is imperative that students of fisheries account for the behaviour of this accumulation in any explanation that may be advanced for changes in the fisheries. The basic laws controlling the volume or magnitude of an accumulation are well known and conform to what has happened to the halibut fishery.

It must be concluded then that in the period 1925 to 1933 on the southern grounds, the amount of fishing is the independent variable and the catch per unit the dependent variable in a relationship in which the annual catch approaches a constant. The annual catch is, however, not a constant and whatever factors fix its volume, it has been fixed at levels above or below the constant at which the stock would remain unchanged — seldom equal to it.

This gives rise to a very practical method of ascertaining the inflow or accretion to the organic reservoir called an accumulated stock. If an excess catch removes part of the stock and a reduced catch restores it, then the removals which will balance the inflow must be between the

two — will in fact be the average of the two catches. This level has been ascertained for the period 1925 to 1933 (Thompson, 1950). Details of the method can be found in that reference.

If then, at any later time, the annual catches are observed to exceed the amount which could be removed without reducing the accumulation characterizing the period 1925 to 1933 and if at that later time no reduction in the accumulation results or if the latter continues to increase, then the usable increment, the inflow to the reservoir from all sources such as birth, growth, etc., must have increased. This in fact happened in 1944, 1945, 1946, and 1947 on the southern grounds; and in 1940 and subsequent years on the western grounds. The catches exceeded the former limit, and no decline appeared.

The test requires accuracy in annual takes recorded as from each stock and it requires that the catch per unit of gear should be comparable during the years when increase or decrease would be expected. Long-term changes in the unit of effort, as between the two periods 1925 to 1933 and 1944 to 1947, for instance, would not invalidate the reasoning. This is fortunate since the technology of a fishery is constantly evolving. The use of an efficiency factor applied uniformly to correct the number of sets over the period of each test would make no difference in the result. Indeed, the use of two entirely different units of effort would suffice as long as each showed the direction of change in stocks within the test period.

The matter is otherwise, of course, if we wish to know at any moment or continuously how near the catch approaches the usable increment. Then it is necessary to determine from the changing catch per unit what the accumulation is at any moment, so that the degree of change can be seen. A factor must be calculated whereby the catch per unit can be multiplied to give the volume of the accumulation. I have tried to calculate this but the details of the calculation are too involved for the present discussion and have no basic significance here.

Since, as is plainly the case in the unregulated fishery, the levels of abundance or magnitude of stock are fixed by economic factors, then it necessarily follows that the effect of natural changes will be visible mainly in the total annual catches. The annual catches from any stock are, however, necessarily equal to the annual net increments from all sources, less what is left to increase the accumulation or plus what is taken from it. The annual net increments include, of course, births, growth, immigration, etc. But as important as any of these, as we know from general biology, is the fact that capture by the fishermen forestalls natural deaths, so that when the stocks are reduced by heavier fishing there is a saving on natural losses. This saving is as truly usable an increment as is growth. It is a phenomenon confronting us in our own lives, that lessened deaths from one cause, pneumonia, leave more to die from another, such as heart disease. All of these known factors must vary with the length of life permitted the fish and, as a consequence, the net productivity of a stock probably varies as the average length of life changes. Hence we must provide for the possibility that each stage

of exploitation must be permitted a different annual catch in case it is to remain stable at that stage. The sum of all the annual increments, net after losses are balanced against gains, can be termed the basic productivity of the stock, that which characterizes the level at which the accumulations are being held.

The evidence for or against change in this basic net productivity of the halibut is in need of close study. It is my proposal that this net productivity be determined empirically, pending complete knowledge of the very complex problems involved in analysis of the stocks and their history. The method can be put in utmost simplicity by an illustration from the southern grounds. (See Figures 3 and 13). The catches for 1918 and 1919 and for 1946 and 1947 of 27 million pounds did not seem to result in reduction of the stocks, and these catches may have been equal to the usable increment at those stages of exploitation. But a catch in excess of $24^1/_2$ millions in the period 1925 to 1933 was in excess of the then usable increment so that a change from 27 to $24^1/_2$ and back to 27 millions may have occurred, whatever its cause. This illustration shows the problem, not only as to the manner in which the change in productivity would show, but as to the statistical weakness of the exact determination of the amount usable without alteration of the accumulation.

I have attempted (T h o m p s o n, 1950, pages 29 and 38) an exact analysis of these changes in productivity by comparing the accumulation of stocks which should have occurred after 1931, had the basic productivity remained unchanged, with the accumulation which actually did occur. The accumulation seems to have been greater everywhere than expected from the excess left by the reduced annual catches as possible additions to it.

Thus before regulation began, the only evidence as to the level of productivity indicates that it had been higher. After regulation began, the figures I have quoted and the more exact analysis not given here (T h o m p s o n, 1950, Figure 8, page 35; Figure 9, page 40; and pages 36 and 41) both indicate a rise in productivity. The increase came when it should have, had it been due to more young in the wake of conserved and hence increased older stocks. But is this merely coincidence? I submit that there is as yet no exact theoretical method of distinguishing the natural and fishery-induced changes in basic productivity other than this coincidence in timing. Although it is possible to distinguish natural and fishery-induced changes in accumulation, there is no clear and recognized method of doing the same for changes in basic productivity aside from timing.

The western grounds also show an increase in this basic productivity over that of the period 1925 to 1936. Thus far the changes there are also what might be expected from restoration of the stocks by regulation of the fishery.

I know as yet of no other adequate methods of approach to the problem of natural versus fishery-caused fluctuations in basic productivity. The suggestion has been advanced that an analysis of the relative

annual increment of young by age determination from samples of the catch would indicate changes in this productivity.

But systems of catch analysis must fall far short of giving a picture of the stocks the fishery samples unless the fishing is evenly distributed. Even though the sampling represents the take of the fishery, it still may fail to reflect the actual changes in stocks because the constituent units of these stocks, such as the young on the "nursery grounds", all tend to vary inversely as the amount of fishing to which they are subject, and this amount of fishing varies widely. The individual bank stock from which the fleet takes least tends to accumulate most in numbers, and vice versa (Thompson, 1950, page 52).

The halibut research abounds with facts which show this. In 1926 and 1927, tagging experiments were conducted during the winter months on the mature stock spawning off Yakutat in the western grounds. The main removals of this segregated and concentrated stock had been made during those winter months. Just prior to the tagging all such winter fishing had been prohibited. The result was, as might have been expected, a very low rate of return from the tagging as this return reflected the great reduction in amount of fishing done on it. It reflected only the fraction of the fishery which was left. This fraction took only the tagged stock caught during the open season. There was, however, a wide dispersal of the stock tagged. But it appears from later experience with the fishery, that whereever such stocks appear during the open fishing season, they are sufficiently different in schooling, in depth inhabited, or character of grounds occupied to allow of discrimination by the fishing fleet in favour of more abundant or less scattered stocks. In other words, that section of the stock tagged in 1926 and 1927 was behaving as a semi-independent accumulation, protected by the closure and removed in part, but not entirely, from the open-season fishery by its habits or distribution. Within the halibut stock of any area there are, therefore, sections which do not mingle completely with others and which are subject to fisheries of different intensity. They may be segregated by habit or by geography, but they are segregated to varying degrees. The catch does not now reflect their actual abundance.

It is vital that this fact be recognized because of the bearing which it has on the calculation of the size of the stocks, either in total or in each section, and on regulation of the fishery.

If, in the experiments of 1926 and 1927, the rate of return of tags was 10 per cent. and it applied to the whole stock, then the catch of the year 1926 should fairly represent 10 per cent. of the stocks on the banks. If the catch in a year was 30 millions of pounds the answer would be a stock on the banks of 300 millions. But this assumes that the rate of return applies to all stocks, which is plainly in error[1]).

It is applied to the particular winter stock tagged, the catch from

[1]) Martin D. Burkenroad. "Fluctuation in abundance of Pacific halibut". Bulletin of the Bingham Oceanographic Collection, Yale University, New Haven. Vol. 11, Art. 4, 1948. pp. 84 and 85.

that may have been nearer 2 millions, and the *spawning stock tagged* was then only 20 millions, a figure very different from the 300 millions calculated above.

This instance is but one of many which have recently come to light. In fact, so evident is this failure of the fishery, as regulated, to utilize all the actual stocks that the system of regulation is being re-examined. The International Fisheries Commission accordingly is investigating the relative distribution of the fishery among the various stocks by a well distributed series of tagging experiments, in an attempt to spread the fishery more uniformly and reasonably, both in time and geographically.

Earlier in this paper, it was stated that the series of near-isolated stocks populating the southern grounds owed their homogeneity and statistical integration to the evenness of the pressure put on them by the well distributed free fishery. The legal restrictions on the fishery have destroyed this evenness of pressure with far-reaching effects and incidentally have thus provided facts which confirm the existence of these constituent stocks, each varying its own way. They incidentally confirm the interpretation of the earlier history of the catch per set which has been advanced by the International Fisheries Commission and the writer.

At present, the increasing abundance has shortened the seasons within which the limited catch can be taken. With these shortened seasons has come a corresponding limitation of the fishery to sections of the stocks characterized by particular age and size compositions, and accordingly by their own seasons of best fishing. It is now believed that these constituent stocks, isolated to varying degrees by age and bank or depth inhabited, exhibit differing stages of accumulation in accord with the differing fishing mortality they suffer. Tagging experiments now show a very low rate of returns from certain grounds; much higher from others more heavily fished. The stocks on these less fished grounds are showing increases but these changes cannot be reflected in the yields because the legal season is not suited to the areas concerned.

The International Fisheries Commission, in Report No. 15 for 1949, calls attention to these facts. A condensation of their findings by D u n l o p and B e l l accompanies this report. They show, within the present stocks, the same type of changes in magnitude which are evident historically, that the volumes or magnitudes of the accumulations on the banks tend to vary inversely as the amount of fishing.

In considering the problem of distorted stocks thus brought to light, it should be taken as one of the consequences of regulation. A free fishery, as already remarked in this paper, is governed by the cost of operation and it reduces all stocks to the level of abundance set by economics regardless of their original levels and seasons of occurrence. It neglects none that are worthy of fishing. It conceivably increases the strain on each stock or section of stock so that the total annual catch of each is an equivalent of the annual increment to it. It admittedly distorts the relative magnitudes of the stocks from what they were in a virgin condition.

In presenting the case of the Pacific halibut for consideration in this report, the author hopes that the extraordinary character of the halibut fishery and the excellent character of the records for a great fishery, with all their defects, will not be forgotten. He feels that such favourable conditions for analysis exist but seldom. It is not just, as is often done, simply because the facts are not obtainable or because they are not understood, to give the impression that fisheries in general have no effect on their stocks.

From the standpoint of general fisheries biology I may add that in halibut and salmon alike, the two most important species on our Northwest Coast, our attention is shifting toward a study of this diversity of accumulated stocks or populations, call them what you will, within the species. In halibut and salmon alike, the species are distorted by the strain of the fishery on the most productive stocks or on those which the law permits to be used. In salmon these semisegregated stocks have been called races, however poor the term may prove to be. This distortion has already given rise to a problem in salmon as to how to utilize for reproduction, in optimum fashion, all the races rather than selected ones. The productive races, at first numerically preponderant because they are adapted to lesser natural mortalities, are heavily fished and given little chance to reproduce. The unproductive stocks on the very margin of existence escape and are even protected to reproduce and take the place of their betters.

Contributions of the International Fisheries Commission and the Writer on Pacific Halibut.

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1931. International Fisheries Commission (U. S. and Canada). "Report". No. 1, Seattle, 1931.

1931. Thompson, William F., Henry A. Dunlop, and F. Heward Bell. "Biological statistics of the Pacific halibut fishery. (1) Changes in yield of a standardized unit of gear". Rep. Int. Fish. Com., No. 6, Vancouver, B. C., 1931.

1934. Thompson, William F., and F. Heward Bell. "Biological statistics of the Pacific halibut fishery. (2) Effect of changes in intensity upon total yield and yield per unit of gear". Rep. Int. Fish. Com., No. 8, Seattle, 1934.

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1950. Thompson, William F. "The effect of fishing on stocks of halibut in the Pacific". Publ. Fish. Res. Inst., Univ. Washington, Seattle, 1950.

1952. Dunlop, Henry A., and F. Heward Bell. "New problems in regulation of Pacific halibut stocks". Journ. du Cons., **18**, 2, pp. 167—71, Copenhague, 1952.

1951. International Fisheries Commission (U. S. and Canada). "Regulation and investigation of the Pacific halibut fishery in 1949". Rep., No. 15, Seattle, 1951.

New Problems in Regulation of Pacific Halibut Stocks.

By

H. A. Dunlop and **F. H. Bell.**

UNDER regulation by the International Fisheries Commission, the abundance of halibut on the Pacific coast has increased almost 150 per cent. since 1931 and annual catches have been increased to over 56 million pounds, about 12 million pounds more annually than immediately before regulation. This additional poundage has added about $ 3,000,000 to the fleets' earnings in each recent year. Though the annual catch is larger, the amount of fishing effort has been reduced about one-third due to the greatly increased abundance.

The success of regulation has created new regulatory problems. The improved condition of the stocks and a doubling in the size of the fishing fleets have greatly increased the rate of landing and sharply reduced the length of the authorized fishing season, in spite of the greater total catch allowed. The fishing season, which was eight and one-half months long in 1932, has progressively declined to only 28 days in Area 2[1]) and 56 days in Area 3 in 1951. Under present conditions, some sections of the stocks are not yielding the poundage of which they are capable. Other sections of the stocks appear to be subjected to too much fishing.

When fishing was conducted over a longer period of the year, the fishermen, guided by experience, fished each ground at the best time from the standpoint of availability of fish, the value of the catches, and weather conditions. With the present season, the fishery tends to concentrate on those grounds where the fish are most available at that time of the year.

The current May fishing period in Area 2 corresponds to the traditionally most productive season of middle Hecate Strait. It misses the best fishing season in lower Hecate Strait and barely touches the beginning or end of the best season on the Cape Scott, Goose Island, and upper Hecate Strait grounds. Historical catch records also show that no other single fishing period of one month will coincide with the most productive season on all these grounds off the British Columbia coast.

[1]) Area 2 extends from Willapa Harbor, Washington, to Cape Spencer, Alaska; Area 3, from Cape Spencer to Bering Sea. These two areas account for over 98 per cent. of the coast's production.

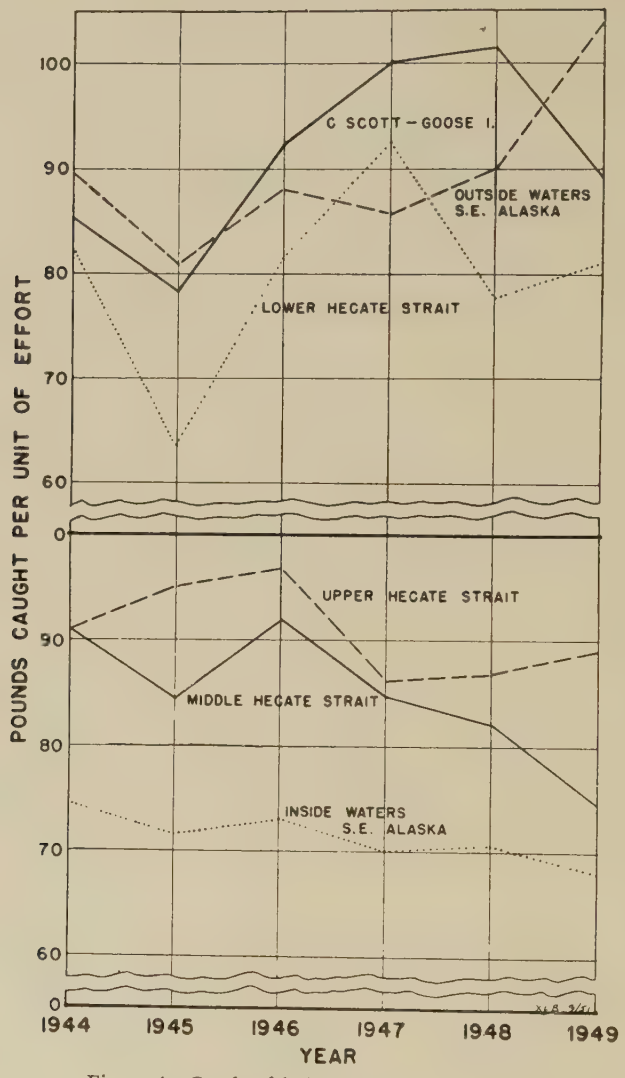

Figure 1. Catch of halibut per unit of effort in subsections of Area 2.

In south-eastern Alaska, fishing tended to be heavier on the sheltered inside grounds in spring and on the exposed outside grounds in summer. Thus, the outside grounds tend to be lightly fished during the present May season.

The increase or decrease in the recent annual catches over earlier years in each of the above sections of the coast tends to vary with the proximity of the present May season to the time of each section's historically best fishing period. In middle Hecate Strait and inside south-eastern

Alaska, where May has always been a month of high production, annual catches are up 96 and 71 per cent., respectively. On the Cape Scott, Goose Island, and upper Hecate Strait grounds, where May was at the beginning or end of the season of high production, the catches have increased only 38 to 48 per cent. On the grounds of lower Hecate Strait and off south-eastern Alaska, where production normally was at a maximum in the summer, the annual catches have declined 48 and 25 % respectively.

Other factors have also affected the distribution of fishing. During the present one-month season in Area 2, vessels of the regular fleet are reluctant to make the longer run to the more distant and exposed grounds of lower Hecate Strait and outside south-eastern Alaska. The possible loss of time from bad weather and tides, coupled with the longer run, could sharply reduce their season's operations. Furthermore, the fleets of small boats, greatly increased in recent years, tend to fish elsewhere than on these exposed offshore grounds.

Fishing records[1]) indicate that there has been a general increase in the abundance of halibut and consequently in the productive capacity of the stocks in the various subsections of Area 2. However, the trend of abundance has not been uniform in all sections of the area in recent years, as is shown by the accompanying chart (Figure 1).

In middle Hecate Strait, where the increase in production has been greatest, the abundance has shown some decline since 1944. In upper Hecate Strait and inside south-eastern Alaska, the abundance has not increased and may have declined. It appears that these regions are now being fished to or beyond their capacity.

In the Cape Scott and Goose Island regions, the improvement in abundance has continued, suggesting that the increased annual catches are not exceeding their present productive capacity.

In lower Hecate Strait and outside south-eastern Alaska, where production has declined despite continued increases in abundance, there is good reason to believe that the full potential catch is not being taken.

In Area 3 the shortening of the season may have had similar effects upon the yield. However, this cannot be demonstrated clearly on account of the relative lack of stability in the distribution of fishing which has resulted from economic factors. Fishing has not been at a stable level in any sections of the area for a sufficient length of time to give an indication of the productive capacity of their stocks.

The above findings regarding the degree of utilization of the stocks of halibut on some grounds in Area 2 imply that the halibut on these grounds form a number of relatively distinct units. This concept of

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[1]) In comparisons of current and earlier fishing records, allowances have been made for changes in the seasonal and other characteristics of the fishery. Uncritical comparison of unadjusted figures may lead to faulty conclusions. For instance, the unadjusted catch per unit of gear in Area 3 for 1949 was 110 pounds. But, as noted on page 21 of the Commission's Report for 1949, studies are under way to correct this figure and "preliminary results indicate that the abundance of halibut in Area 3 in 1949 was actually more than 100 per cent. above the 1930 level". The catch, in terms of 1930 fishing, was thus about 130 pounds per unit of effort rather than 110.

conditions is not new, as is indicated by the following quotation from a discussion of the division of the coast into areas in Commission Circular No. 5 (1937), which was based on extensive scientific reports issued by the Commission.

> "The stock in Area 2 is however composed of several units that are not only independent of the Area 3 stock but also of one another. These separate Area 2 units could be regulated as separate stocks but because they are all in about the same condition, they can also be regulated together. It is desirable to have as few regulatory areas as possible, so the more or less distinct small units in the Area 2 stock have been treated as a single large unit."

Much biological evidence, published and unpublished, is at hand to demonstrate a very limited interchange of stocks between Areas 2 and 3 and between subsections of Area 2. Some of this evidence is as follows:—

1. Various grounds within the areas are characterized by distinctive size-classes of halibut which have persisted since the earliest years for which records are available.
2. Morphometric studies conducted on scattered grounds in Area 2 indicated that their populations did not mingle to any significant extent, at least until the approach of maturity.
3. Tagging experiments on immature stocks in Area 2 showed very little movement from bank to bank more than 50 miles apart.
4. Tagging experiments on spawning grounds in Area 2 showed that the mature fish migrated within relatively restricted sections of the area adjacent to the place of marking and were not dispersed evenly throughout the area.
5. Current tagging experiments in Area 2 indicate that the stocks on the grounds at different times of the year are not all equally available to the fishery during the present fishing season.
6. Recent differences in the trends of abundance in different sections of Area 2 tend to correspond inversely to the amounts of fishing being conducted on them.

To provide quantitative data regarding the present utilization of the stocks, a broad tagging programme is in progress. It provides for tagging on different important banks in Areas 2 and 3 at different times of year. The results will show what geographic and seasonal changes in the distribution of fishing may be necessary to secure full utilization.

Recoveries of tags during 1947, 1948, and 1949 (Reports 13, 14, and 15) from most recent experiments show that the stocks on different grounds are in fact contributing very unequally to the catch from Area 2 as a whole. Since almost every recovery was made on the bank where the fish was originally marked and released, wide differences in the rate of recovery of tags released on different banks during the fishing season indicate great inequalities in exploitation during the present May season. Differences in the rate of recovery of tags released on the same bank in different months also suggest that other inequalities result from

different sections of the stocks being available to the fishery at different seasons of the year.

Preliminary results show a wide difference in the availability of halibut, marked on different grounds in the same month and on the same ground in different months, to the present May fishery. They suggest that utilization may require fishing to some degree at least from late April through August.

Since the halibut treaty permits only one fishing period in each area each year, there are but two types of regulatory measures that might provide a partial solution to the problem of achieving the maximum sustained yield from the stocks; namely, the rotation of opening dates over a period of years and/or the opening of different sections of the grounds as distinct areas at different seasons of the year from time to time.

In 1951 the Forrester Island section of the outside grounds of south-eastern Alaska and a portion of lower Hecate Strait were opened as separate regulatory areas for a limited period of time about two months after the end of the regular Area 2 season.

Approximately 2·5 million pounds were removed from the lower Hecate Strait area compared to the 1·0 million pounds removed from the same grounds during the May 1950 season. From the Forrester Island grounds, about 1·0 million pounds were removed compared to about 0·25 million pounds during the regular season in 1950. Thus, in these two limited sections of the coast, a net gain in yield of about 2·25 million pounds was achieved, which was in accord with expectations.

The catches from these areas contained a very high proportion of large-sized fish, indicating an accumulation of their stocks such as would result from underfishing. The absence of tag recoveries from fish marked on other grounds supports the belief that the stocks fished were not migrants from other grounds already being heavily fished.

There are other sections of Area 2 whose May stocks do not now appear to be adequately exploited, and which might be expected to yield about two and one-quarter million pounds more than at present. Another three million pounds might be secured by exploiting later or earlier appearing stocks on grounds whose May stocks are now being adequately fished. About one and one-half million pounds more might also result from spreading catches over a longer season, thus permitting a larger proportion of the fish taken each year to acquire more of their summer growth before capture. To what extent the objective of securing this additional poundage may be achieved will depend upon the flexibility of regulatory authority and upon operational conditions in the fishery itself.

Some modification of the system of management, applied so successfully by the International Fisheries Commission since 1932, will be necessary if the maximum productive capacity of the Pacific halibut stocks is to be reached.

Analysis of the Icelandic Herring during the Year 1950.

By

Hermann Einarsson.

Introduction.

In two earlier papers (Einarsson 1949, 1951) it was shown that racial analysis of Icelandic herring can be carried out by means of the otoliths, the core characteristics of the otoliths being used as distinguishing features. The problems involved and the difficulties encountered were discussed at length in the latter paper, to which it may suffice to refer.

During 1950 the otolith method of racial analysis was successfully applied, and still better agreement between maturity stage and otolith type was obtained, because the dominant year-classes had already spawned once or twice or were developing their sexual products for the first time, while during 1949 a considerable part of the collection consisted of immature herring in maturity stage II—III, which we had difficulty in distinguishing from stage VIII.

The importance of counting the spawning zones in the otoliths, for such can be clearly distinguished in older herrings, has been realized since the beginning of this work. But hitherto the material has been unsuitable for such an analysis, since the 1949 material comprised mostly immature herring and the 1950 material mostly first-time spawners, but as is well known from work on cod otoliths and scales of herring the first spawning zone offers the greatest difficulty.

A closer study of the limitations of the otolith method was desirable. This study was made during the period when maturity stages indicate the race. The analysis of vertebral numbers has also been carried out during this year, for further support of our racial grouping. But it is considered appropriate to devote less time to this work in the future. Age determinations have been made by otolith readings, which proved easier than scale readings.

The present study comprises data on 5504 herrings, which were caught in Jökuldjúp, Miðnessjór, and Grindavíkursjór during the period 13. August 1950 to 5. January 1951.

For assistance during the preparation of this paper I am greatly indebted to Mrs. Hulda Jónasdóttir. For correcting my English and valuable suggestions my thanks are due to Mr. B. B. Parrish, Aberdeen.

Racial Analysis.

The otolith sample was divided into two parts; that including otoliths collected in the earlier period when the maturity stages are unreliable as a guide to race, and that comprising those collected in the latter period where there is generally very good agreement between maturity stages and otolith types. These two periods will now be considered separately.

A. First period, from 13. August to 18. October.

a) Maturity stages. During this period we noted the maturity stages shown below. These were tested for vertebral number with the following results:—

Number of Vertebrae	Maturity Stage II	II-III	III	III-IV	IV	V	VI	VII	VII-VIII	VIII	Total
60	—	—	—	—	—	—	—	—	—	1	1
59	—	—	23	—	3	—	—	—	—	13	39
58	6	1	459	53	152	—	—	2	9	375	1057
57	67	7	941	59	260	1	1	5	31	1220	2592
56	24	—	143	10	33	—	—	2	8	275	495
55	—	—	5	—	—	—	—	—	—	4	9
54	—	—	1	—	—	—	—	—	1	2	4
Number	97	8	1572	122	448	1	1	9	49	1890	4197

	II	III	III-IV	IV	VII-VIII	VIII	Total
M	56·814	57·222	57·352	57·279	56·980	57·061	57·146
δ	0·524	0·641	0·626	0·600	0·729	0·624	0·636
m	±0·053	± 0·016	± 0·057	± 0·028	± 0·104	± 0·014	± 0·009

The vertebral numbers show clearly that the II-stage specimens belong to the summer spawning race (for which the average number of vertebrae in 1949 was 56·959 ± 0·009), while the specimens in maturity stages III, III—IV, and IV belong to the spring spawners (for which the average number of vertebrae in 1949 was 57·234 ± 0·015). On the other hand it is evident from the mean of the VIII-stage specimens that these belong to both races.

b) Analysis of otoliths. The division of the collection according to race as shown by the otolith analysis is illustrated in the tables on page 174.

The vertebral numbers found give strong support to the correctness of our analysis. The maturity stages show that during this period the spring spawners are developing their genital organs, being in stages III, III—IV, and IV, while a considerable number still remain in stage VIII, and cannot be distinguished from the summer spawners by the degree

Spring Spawners.

Number of Vertebrae	Maturity Stage II	II-III	III	III-IV	IV	V	VIII	Total
60	—	—	—	—	—	—	1	1
59	—	—	23	—	3	—	7	33
58	4	1	458	53	152	—	249	917
57	14	5	940	59	260	1	513	1792
56	1	—	143	10	33	—	86	273
55	—	—	5	—	—	—	—	5
54	—	—	1	—	—	—	2	3
Number	19	6	1570	122	448	1	858	3024
M			57·222	57·352	57·279		57·203	57·229
δ			0·641	0·626	0·600		0·643	0·636
m			± 0·016	± 0·057	± 0·028		± 0·022	± 0·011

Summer Spawners.

Number of Vertebrae	Maturity Stage II	II-III	III	VI	VII	VII-VIII	VIII	Total
59	—	—	—	—	—	—	6	6
58	2	—	1	—	2	9	126	140
57	53	2	1	1	5	31	707	800
56	23	—	—	—	2	8	189	222
55	—	—	—	—	—	—	4	4
54	—	—	—	—	—	1	—	1
Number	78	2	2	1	9	49	1032	1173
M	56·731					56·980	56·943	56·931
δ	0·498					0·729	0·584	0·584
m	±0·056					±0·103	±0·018	±0·018

of maturity. Most of the summer spawners are in stage VIII, but in the beginning of the period we also encounter summer spawners that have just finished spawning (stages VII and VII—VIII) or are immature.

In the next table the various otolith types are tested for vertebral number. The arithmetic means are quite typical for the two respective races and do not differ significantly within the same race. On the other hand significant differences are found between the vertebral numbers of otolith types belonging to different races.

Number of Vertebrae	Otolith Type SA	SB	SC	SD	Total S	VA	VB	VC	Total V
60	—	—	—	—	—	—	1	—	1
59	4	—	1	1	6	15	16	2	33
58	59	48	16	17	140	484	354	78	917
57	338	199	114	149	800	940	706	147	1792
56	91	48	34	49	222	163	95	15	273
55	2	1	1	—	4	3	2	—	5
54	1	—	—	—	1	2	1	—	3
Number	495	296	166	216	1173	1607	1175	242	3024
M	56·937	56·993	56·892	56·861	56·931	57·211	57·244	57·277	57·229
δ	0·605	0·581	0·580	0·454	0·587	0·644	0·632	0·583	0·636
m	±0·027	±0·034	±0·045	±0·031	±0·017	±0·016	±0·018	±0·037	±0·011

B. Second period, from 11. November to 5. January.

a) Maturity stages. During this period the maturity stages generally indicate the race. This is seen in the following table which gives the vertebral numbers of the different maturity stages:—

Number of Vertebrae	Maturity Stage II	II-III	III	IV	IV-V	V	VIII	Total
59	—	—	—	2	—	2	1	5
58	3	—	2	175	—	49	78	307
57	12	2	16	322	1	79	384	816
56	6	—	3	46	—	13	107	175
55	—	—	—	—	—	3	1	4
Number	21	2	21	545	1	146	571	1307
M				57·244		57·232	56·949	57·103
δ				0·601		0·713	0·580	0·620
m				±0·026		±0·059	±0·024	±0·017

The collection was grouped according to otoliths, with the following result:—

Spring Spawners

Number of Vertebrae	Maturity Stage III	IV	IV-V	V	Total
59	—	2	—	2	4
58	2	175	—	49	226
57	15	322	1	79	417
56	3	46	—	13	62
55	—	—	—	3	3
Number	20	545	1	146	712
M		57·244		57·232	57·233
δ		0·601		0·713	0·624
m		±0·026		±0·059	±0·023

Summer Spawners

Number of Vertebrae	Maturity Stage II	II-III	III	VIII	Total
59	—	—	—	1	1
58	3	—	—	78	81
57	12	2	1	384	399
56	6	—	—	107	113
55	—	—	—	1	1
Number	21	2	1	571	595
M				56·949	56·946
δ				0·580	0·580
m				±0·024	±0·024

It will be seen that during this period the maturity clearly distinguishes the spring spawners, which are in maturity stages III, IV, and V, from the summer spawners, which are mostly in stage VIII.

b) The **analysis of otolith** types shows the following results, which are in accordance with our previous findings.

Number of Vertebrae	Otolith Type SA	SB	SC	SD	Total S	VA	VB	VC	Total V
59	—	1	—	—	1	—	3	1	4
58	24	21	13	23	81	105	83	38	226
57	147	83	67	102	399	209	159	49	417
56	45	20	20	28	113	31	23	8	62
55	—	—	—	1	1	3	—	—	3
Number	216	125	100	154	595	348	268	96	712
M	56·903	57·024	56·930	56·955	56·946	57·195	57·246	57·333	57·233
δ	0·557	0·600	0·570	0·596	0·580	0·622	0·616	0·640	0·624
m	±0·038	±0·053	±0·057	±0·048	±0·024	±0·033	±0·037	±0·065	±0·023

C. Review of results.

a) Maturity stages. In the course of our investigation we encountered all maturity stages with the exception of stage I, only found in young herring, which were not included in the present study. This will be seen by the following table, which summarizes the whole of the material:—

Number of Vertebrae	Maturity Stage II	II-III	III	III-IV	IV	IV-V	V	VI	VII	VII-VIII	VIII	Total
60	—	—	—	—	—	—	—	—	—	—	1	1
59	—	—	23	—	5	—	2	—	—	—	14	44
58	9	1	461	53	327	—	49	—	2	9	453	1364
57	79	9	957	59	582	1	80	1	5	31	1604	3408
56	30	—	146	10	79	—	13	—	2	8	382	670
55	—	—	5	—	—	—	3	—	—	—	5	13
54	—	—	1	—	—	—	—	—	—	1	2	4
Number	118	10	1593	122	993	1	147	1	9	49	2461	5504

	III	III-IV	IV-V	V	VII-VIII	VIII	Total
M	57·218	57·352	57·260	57·231	56·980	57·035	57·139
δ	0·640	0·626	0·602	0·711	0·729	0·616	0·632
m	±0·016	±0·057	±0·019	±0·059	±0·104	±0·012	±0·008

b) Otolith analysis. We have divided the whole collection by the otolith method as shown in the two following tables, in which vertebral numbers are also assigned to each maturity stage:—

Spring Spawners

Number of Vertebrae	Maturity Stage II	II-III	III	III-IV	IV	IV-V	V	VIII	Total
60	—	—	—	—	—	—	—	1	1
59	—	—	23	—	5	—	2	7	37
58	4	1	460	53	327	—	49	249	1143
57	14	5	955	59	582	1	80	513	2209
56	1	—	146	10	79	—	13	86	335
55	—	—	5	—	—	—	3	—	8
54	—	—	1	—	—	—	—	2	3
Number	19	6	1590	122	993	1	147	858	3736
M			57·218	57·352	57·260		57·231	57·203	57·230
δ			0·640	0·626	0·602		0·711	0·643	0·631
m			±0·016	±0·057	±0·019		±0·059	±0·022	±0·011

Summer Spawners

Number of Vertebrae	Maturity Stage II	II-III	III	VI	VII	VII-VIII	VIII	Total
59	—	—	—	—	—	—	7	7
58	5	—	1	—	2	9	204	221
57	65	4	2	1	5	31	1091	1199
56	29	—	—	—	2	8	296	335
55	—	—	—	—	—	—	5	5
54	—	—	—	—	—	1	—	1
Number	99	4	3	1	9	49	1603	1768
M	56·758					56·980	56·945	56·936
δ	0·534					0·729	0·582	0·586
m	±0·054					±0·104	±0·014	±0·014

These data show that during late summer and early winter, the developing maturity stages (III—V) characterize the spring spawners, and during late summer both races are encountered in maturity stage VIII, in which condition the major part of the summer spawners remain throughout the period of investigation.

Next, vertebral numbers have been assigned to the various otolith types encountered in the material, as shown in the following table:—

Number of Vertebrae	Otolith Type SA	SB	SC	SD	Total S	VA	VB	VC	Total V
60	—	—	—	—	—	—	1	—	1
59	4	1	1	1	7	15	19	3	37
58	83	69	29	40	221	589	437	116	1143
57	485	282	181	251	1199	1149	865	196	2209
56	136	68	54	77	335	194	118	23	335
55	2	1	1	1	5	6	2	—	8
54	1	—	—	—	1	2	1	—	3
Number	711	421	266	370	1768	1955	1443	338	3736
M	56·927	57·002	56·906	56·900	56·936	57·208	57·245	57·293	57·230
δ	0·591	0·586	0·577	0·573	0·586	0·640	0·628	0·601	0·631
m	±0·022	±0·028	±0·035	±0·030	±0·014	±0·014	±0·016	±0·033	±0·011

We have also made a comparison of each pair of means by calculating the factor $\frac{d}{\delta d}$ for each pair, where $d = M_1 — M_2$ and

$$\delta d = \sqrt{\frac{N_1}{N_2} m_1^2 + \frac{N_2}{N_1} m_2^2}.$$

The difference between the means is significant with 99·5 % certainty when the value exceeds 3. The values found are shown in the following table:—

	VC	VB	VA	SD	SC	SB	SA
SA	*9·38*	*11·77*	*10·41*	0·24	0·50	2·08	
SB	*6·77*	*7·36*	*6·24*	2·49	2·13		
SC	*8·06*	*8·47*	*7·55*	0·13			
SD	*8·93*	*9·86*	*8·88*				
VA	2·36	1·74					
VB	1·30						

Significant differences between mean vertebral counts are found between otolith types belonging to different races, while the differences are not significant at the 99·5 % level when otolith types belonging to the same race are compared. The value found for the difference between total V and total S is 15·7.

Whereas the vertebral numbers of the S types do not show any clear trends, it was mentioned earlier (Einarsson 1951 p. 68) that the atypical V types (VB and VC) seem to have a higher mean than the VA type. This was also found in the collection under consideration. The values found during 1949 and 1950 were as follows:—

3. period 1949	VA: 57·245 ± 0·021	VB+VC: 57·265 ± 0·024	
4. period 1949	VA: 57·188 ± 0·027	VB+VC: 57·229 ± 0·031	
1. period 1950	VA: 57·211 ± 0·016	VB: 57·244 ± 0·018	VC: 57·277 ± 0·037
2. period 1950	VA: 57·195 ± 0·033	VB: 57·246 ± 0·037	VC: 57·333 ± 0·065

It was suggested that these differences might indicate that the atypical V types were hatched at somewhat lower temperatures than the VA type.

The frequency of occurrence of the different otolith types has also been calculated. During 1949 we found a very close agreement between the percentage frequencies of the otolith types during different periods. These percentages are shown together with the 1950 figures in the following table:—

Type/Period	1949			1950		
	3.	4.	Total	1.	2.	Total
SA	46·3	46·4	47·4	42·2	36·3	40·2
SB	26·3	18·3	23·3	25·5	21·0	23·8
SC	9·6	12·1	10·7	14·2	16·8	15·0
SD	17·8	23·2	18·7	18·4	25·9	20·9
VA	56·2	57·8	56·8	53·1	48·9	52·3
VB+VC	43·8	42·2	43·2	46·9	51·1	47·7

If allowance is made for the vagueness of the definition of the atypical otoliths, there seems to be good agreement between the values found. However, there seems to be a real difference between the frequency of the SA and SD types during the second period in 1950, compared with the earlier periods.

The Change in Maturity during the Period of Investigation.

The change in maturity during the period of investigation is shown for spring spawners and summer spawners in Figure 1. These diagrams should be compared with Figure 9 in my earlier paper (Einarsson 1951, p. 69) which shows corrresponding results for 1949.

An outstanding difference from the 1949 results is that II-stage specimens were more numerous in 1949 than in 1950. Undoubtedly this is due to the fact, mentioned earlier, that a considerable part of the 4-ringers, which in 1949 constituted about 70 % of the catches, consisted of herring that had not spawned before but which spawned for the first time in 1950. With this exception the changes in maturity in

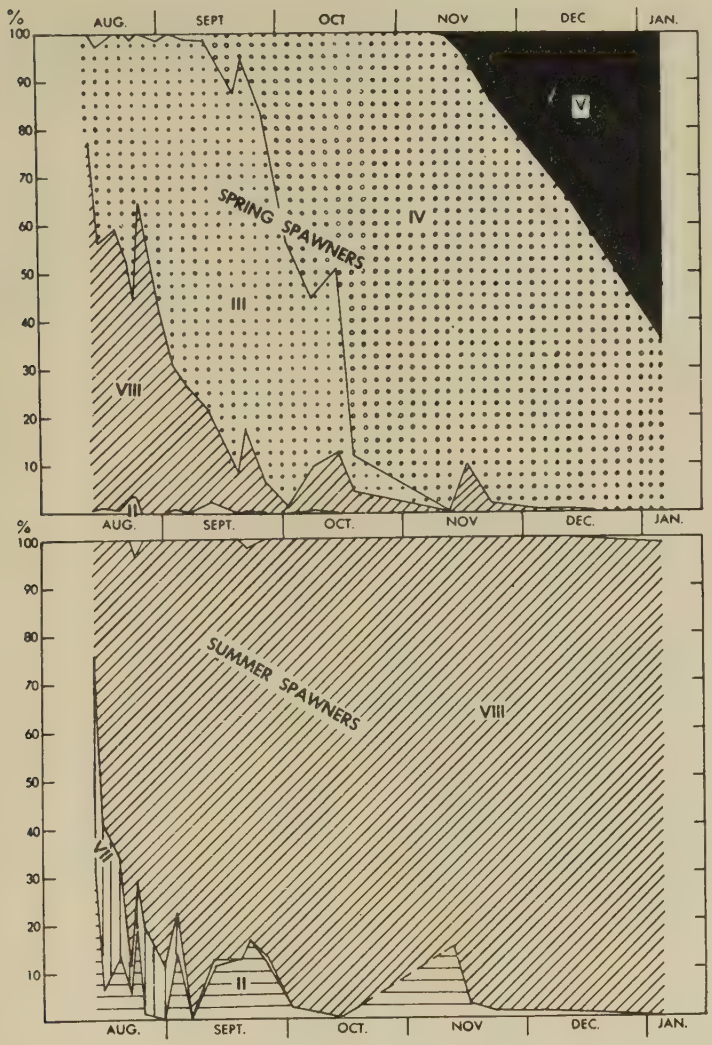

Figure 1. Percentage frequency of maturity stages during the period of investigation.

the two years were similar. Both races were encountered in stage VIII until about the middle of October, when the last spring spawners entered stage III, while the summer spawners were in stage VIII during the whole period. The conclusions previously set forth are thus fully confirmed by the present investigation.

Limitations of the Otolith Method.

Obviously we must expect some error in the determination of the otolith types. Hitherto difficult otoliths have been included in our analyses, although it was realized that sometimes certain otoliths might belong to either of the two races. Totally wrong determinations could also be expected.

An opportunity to estimate these errors occurs during the period when the degree of maturity indicates the race and when there is small admixture of immature herrings in the catches. Both these requirements were fullfilled during the second period of investigation in 1950. A note was made of the uncertain otoliths encountered in the course of the investigation and when the otolith type did not agree with the degree of maturity. The results of this study are expressed in the following table:—

Otolith type determined	Type decided on second inspection, regard being taken to degree of maturity.						
	VA	VB	VC	SA	SB	SC	SD
VA	16	—	—	—	—	—	16
VB	—	4	—	—	—	12	1
VC	—	—	6	—	14	1	—
SA	—	—	—	1	—	—	—
SB	—	1	24	—	2	—	—
SC	—	—	1	—	—	1	—
SD	13	—	—	—	—	—	3

This makes a total of 116 uncertain or wrong determinations out of a total of 2370, or 4·9 %. It will be seen that the SB and VC types are most difficult to distinguish. The following list shows how the uncertain or wrong determinations are divided among the samples.

Sample No.	Number of Specimens	Number of uncertain or wrong determinations	Percentage of uncertain otoliths	Sample No.	Number of Specimens	Number of uncertain or wrong determinations	Percentage of uncertain otoliths
14/50	274	14	5·1	21/50	167	8	4·8
15/50	249	12	4·8	22/50	248	12	4·8
16/50	242	14	5·8	23/50	198	11	5·6
17/50	298	12	4·0				
18/50	247	13	5·3	1/51	199	9	4·5
20/50	248	11	4·4	Total:	2370	116	4·9

It will be seen that the percentage error is fairly constant. It will also be seen from the above table that 44 otoliths were incorrectly referred to the V types when they should have been included in the S types, while 39 otoliths were incorrectly referred to the S types when they should have been reckoned as V type. Thus the errors are almost equally divided between the types and we can expect the race frequencies to be almost correct in spite of these errors. In any case it is obvious that the errors in the determinations do not endanger the results, as previously maintained.

Racial Stability.

A few remarks are necessary on an assumption previously made. It was assumed "that a herring hatched in spring also spawns in spring and a herring of summer progeny also spawns during summer. In other words, there are no 'crossings over' from race to race." (Einarsson 1951, p. 63).

A different view is held by Storrow (1920) and Hodgson (1925, 1929), who maintain, with regard to herring of the North Sea, that the occurrence of separate races is an impossibility. They base this opinion on investigation of the growth of the herring before formation of the first winter-ring, as calculated from the size of the central area of the scale. Hodgson points out that "the '8' and '9—11' cm. (l_1) groups of fish were always found spawning together and the resulting fry would be a heterogeneous group" (l.c., 1929, p. 64).

Johansen (1929, pp. 90—91) opposes this opinion. Criticizing Storrow's conclusions, he puts forth arguments that may be summed up as follows:— If l_1 of an *autumn spawner* is small, either (1) the fish may have been hatched early in the season and formed a winter ring during its first winter of life, or (2) it may have been hatched late in the season and had a proportionately small growth during the first year. On the other hand, large central areas in the scales of *spring spawners* (3) may be the result of early hatching and the quickest growing of these fish will probably be larger than the slowest growing autumn spawners.

Applied to the Icelandic herring problems I think possibility (1) is seldom realized and such scales can be distinguished, as pointed out by Hodgson (1929, p. 65). The two other alternatives are both possible in my opinion, but Hodgson (l.c., p. 65) maintains that "the suggestion that the quickest growing spring fish are probably larger than slowest growing autumn fish when the first ring is formed, although the latter fish are six months older, is surely almost beyond the bounds of possibility."

However, we must bear in mind that in the six months span we include the winter months, in which growth ceases or is exceedingly slow. But to the alternatives mentioned by Johansen we can add one, which I think is of most importance in Icelandic waters. This is the fact that *in Icelandic waters we have very different growth conditions and the larval stock carried to one area (for instance, the northern fjords) may encounter less favourable growth conditions than the larval stock carried to another (for instance, the oceanic waters or the southern coastal grounds).* The result of this will undoubtedly be that autumn spawners carried to an inferior growth area will have a similar size or be even smaller at the formation of the first winter-ring than spring spawners carried to the superior growth area.

Growth calculations of Icelandic herrings show that the values of l_1 for the two races overlap to a very great extent (Einarsson 1951, p. 58, Fig. 2) and I concluded that the size of the central area of the

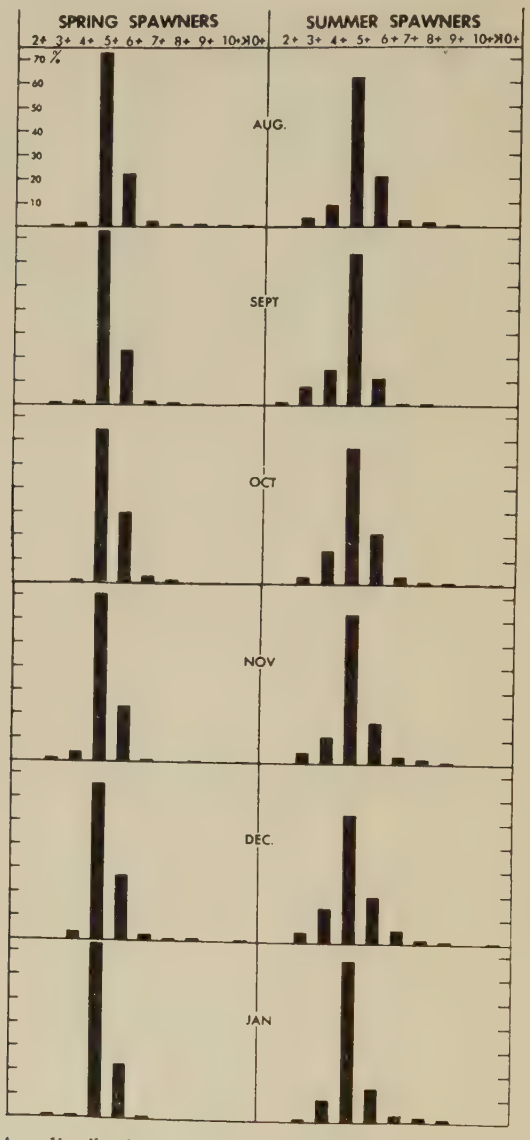

Figure 2. Age distribution of the southern Icelandic herring during 1950.

scale was a poor criterion of the race. Observations on the size of the central area of the otoliths also accord with this statement.

As a result of the above analysis of the otolith readings I can add some further comment on this problem, for it is obviously possible to test the assumption mentioned by otolith types. For this purpose the SA type is most advantageous, as it can hardly be confused with any other type. *If the spring spawners are heterogeneous, i.e., consist of*

Age Distribution of the Icelandic Herring during 1950.

Spring Spawners.

Sample No.	Age	3+	4+	5+	6+	7+	8+	9+	10+	>10+	Total
1/50		—	—	123	29	2	—	1	1	—	156
2/50		—	1	122	37	5	1	—	—	1	167
3/50		—	6	98	39	5	2	1	—	—	151
4/50		—	2	62	15	1	—	—	—	—	80
5/50		3	5	128	33	2	1	—	—	1	173
6/50		—	4	81	32	3	—	2	—	—	122
7/50		—	—	122	34	2	2	1	—	—	161
8/50		1	4	175	52	4	—	—	—	—	236
9/50		1	2	228	79	3	—	—	—	1	314
10/50		5	6	189	45	3	1	1	—	—	250
11/50		—	3	171	66	4	4	1	—	—	249
12/50		1	2	125	23	1	2	—	—	—	154
13/50		2	3	171	35	2	1	—	—	—	214
14/50		—	1	150	74	7	3	—	—	—	235
15/50		—	3	100	36	4	4	—	—	—	147
16/50		—	1	30	7	1	—	—	—	—	39
17/50		—	2	107	60	5	2	—	—	—	176
18/50		—	6	104	40	—	—	—	—	1	151
20/50		5	8	111	30	3	—	1	—	—	158
21/50		—	3	71	24	—	—	—	—	—	98
22/50		—	4	81	25	2	1	—	—	1	114
23/50		—	5	60	33	2	—	2	—	—	102
1/51		1	2	65	20	1	—	—	—	—	89
		19	73	2674	868	62	24	10	1	5	3736
	%	0·5	2·0	71·6	23·2	1·6	0·6	0·3	0·0	0·2	100·0

Summer Spawners.

Sample No.	2+	3+	4+	5+	6+	7+	8+	9+	10+	>10+	Total	% V : S
1/50	—	1	1	19	2	1	1	—	—	—	25	86 : 14
2/50	—	—	4	19	7	1	—	—	—	—	31	84 : 16
3/50	—	1	2	9	3	—	—	—	—	—	15	90 : 10
4/50	—	—	6	49	11	2	1	—	—	—	69	53 : 47
5/50	—	6	3	15	1	1	—	—	—	—	26	87 : 13
6/50	—	—	4	42	26	2	3	1	—	—	78	60 : 40
7/50	—	2	5	20	7	1	—	—	—	—	35	82 : 18
8/50	—	13	12	30	3	—	—	—	—	—	58	80 : 20
9/50	—	1	4	34	14	1	—	—	—	—	54	85 : 15
10/50	1	3	17	60	7	—	—	—	—	—	88	74 : 26
11/50	2	6	6	21	5	1	—	—	—	—	41	86 : 14
12/50	1	7	15	69	7	1	1	—	—	—	101	60 : 40
13/50	1	4	10	58	11	1	1	—	—	—	86	71 : 29
14/50	—	—	6	18	12	3	—	—	—	—	39	86 : 14
15/50	—	—	8	60	28	5	—	1	—	—	102	59 : 41
16/50	—	15	37	117	22	6	4	1	1	—	203	16 : 84
17/50	—	—	13	69	36	2	1	—	—	1	122	59 : 41
18/50	—	1	8	60	22	3	2	—	—	—	96	61 : 39
20/50	—	9	12	53	12	3	1	—	—	—	90	64 : 36
21/50	—	1	8	46	9	3	1	1	—	—	69	58 : 42
22/50	—	10	19	65	27	11	1	1	—	—	134	46 : 54
23/50	—	1	15	58	18	1	2	—	—	1	96	52 : 48
1/51	—	1	10	74	16	4	3	2	—	—	110	44 : 56
	5	82	225	1066	306	53	22	7	1	2	1768	
%	0·3	4·6	12·7	60·3	17·3	3·0	1·2	0·4	0·1	0·1	100·0	

herrings hatched during both spring and summer, we should encounter herrings with otoliths of the SA type in maturity stage IV or V during the period November to January. This would indicate that the herrings had been hatched during summer, but were going to spawn in spring.

Of 711 SA otolith pairs I found only one pair (No. 92 in sample 20/50) which was from a herring in these maturity stages (stage IV). However, in spite of this one exception, I feel justified in stating that interchange between populations, i.e., summer spawners becoming spring spawners or vice versa, must be very rare. Therefore I regard the two seasonal herring races in Icelandic waters as stable units. The Icelandic races are perhaps genotypically distinct and not merely phenotypically distinct, as investigations on meristic characters indicate. This view finds support in the life history of the Icelandic herring, which has two fairly distinct spawning periods. This matter will be discussed in detail in a later paper.

I am inclined to think that the intermediate, and therefore difficult, otolith types are formed under local conditions, resembling those in which the other race passes the post-larval stage. But we cannot exclude the possibility that the uncertain otoliths belong to herrings which have reverted from one race to another, and that these otoliths are thus signs of interchange between the populations. This would undoubtedly explain some of the discrepancies between otolith type and maturity stage, but positive evidence to this effect has not yet been procured.

Age Composition.

In a preliminary report published in *Annales Biologiques* Vol. VII, 1951, a survey of the age distribution and vertebral numbers of different year-classes was given. In the above table (see p. 183) the detailed results of the age determinations are presented and Figure 2 shows the age composition from month to month during the period of investigation. The variations from one month to another are very slight indeed, and the extraordinary strength of the year-classes from the summer of 1944 and the spring of 1945 (the 5-ringers) is evident. During this year recruitment was very slight.

Units of the Herring Population.

It was discovered during 1949 that the races occur repeatedly in approximately the same proportions. This phenomenon was also encountered during the year under discussion. The following mixtures were found:—

1. 85 % spring spawners : 15 % summer spawners.

Nine samples of this unit were taken in Grindavíkursjór, 13. Aug. (86 : 14), 15. Aug. (84 : 16), 19. Aug. (90 : 10), 23. Aug. (87 : 13), 30. Aug. (82 : 18), 3. Sept. (80 : 20); Miðnessjór, 7. Sept. (85 : 15); Grindavíkursjór, 19. Sept. (86 : 14); Jökuldjúp, 2. Oct. (86 : 14).

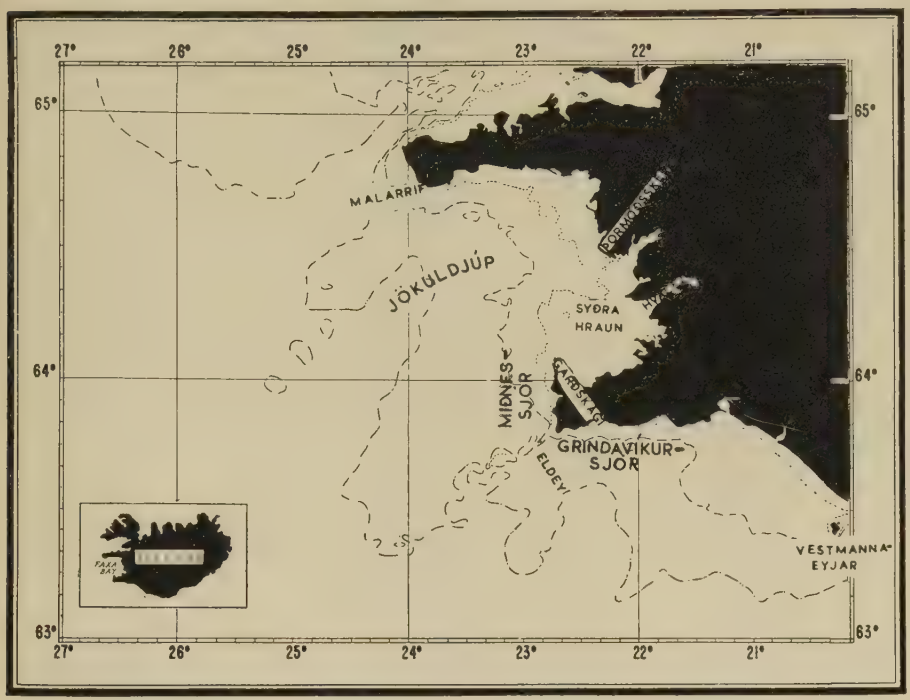

Figure 3. Icelandic localities mentioned in the text.

2. 72 % spring spawners : 28 % summer spawners.
Two samples of this unit were taken in Miðnessjór, 12. Sept. (74 : 26), and in Jökuldjúp, 26. Sept. (71 : 29).

3. 58 % spring spawners : 42 % summer spawners.
Nine samples of this unit were taken in Miðnessjór, 22. Aug. (53 : 47); Grindavíkursjór, 25. Aug. (60 : 40); Jökuldjúp, 21. Sept. (60 : 40); Grindavíkursjór, 8. Oct. (59 : 41); off Eldy, 18. Oct. (59 : 41); Miðnessjór, 12.Nov. (61 : 39), 16. Nov. (64 : 36), 23. Nov. (58 : 42), and 13. Dec. (52 : 48).

4. 45 % spring spawners : 55 % summer spawners.
Two samples of this unit were taken off Garðskagi, 4. Dec. (46 : 54) and off Reykjanes, 5. Jan. 1951 (44 : 56).

5. 16 % spring spawners : 84 % summer spawners.
One sample showing this composition was taken in Jökuldjúp, 14. Oct.

During 1949 we found the summer spawners in the majority, but in 1950 the spring spawners were most numerous, which shows that our sampling cannot be completely representative for the stock as a whole. The fishery was to a greater degree carried out in Grindavíkursjór and

List of Samples examined.

Sample No.	Date (1950)	Locality	Number examined
F 1/50	13/8	Grindavíkursjór	181
F 2/50	15/8	Grindavíkursjór	198
F 3/50	19/8	Grindavíkursjór	166
F 4/50	22/8	Miðnessjór	149
F 5/50	23/8	Grindavíkursjór	199
F 6/50	25/8	Grindavíkursjór	200
F 7/50	30/8	Grindavíkursjór	196
F 8/50	3/9	Grindavíkursjór	294
F 9/50	7/9	Miðnessjór	368
F 10/50	12/9	Miðnessjór	338
F 11/50	19/9	Grindavíkursjór	290
F 12/50	21/9	Jökuldjúp	255
F 13/50	26/9	Jökuldjúp	300
F 14/50	2/10	Jökuldjúp	274
F 15/50	8/10	Grindavíkursjór	249
F 16/50	14/10	Jökuldjúp	242
F 17/50	18/10	Off Eldey	298
F 18/50	12/11	Miðnessjór	247
F 20/50	16/11	Miðnessjór	248
F 21/50	23/11	Miðnessjór	167
F 22/50	4/12	Off Garðskagi	248
F 23/50	13/12	Miðnessjór	198
F 1/51	5/1	Off Reykjanes	199

Miðnessjór, and in these regions in 1949 also the spring spawners were more numerous than the summer spawners. It will be interesting to see if this is maintained in the future.

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On the Migration of the Elver (*Anguilla vulgaris* Turt.) at Sea.

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Introduction.

After the enclosure of the Zuyder Zee in 1932, it soon appeared that in the newly formed freshwater Lake Yssel the eel population developed very well, and big catches were made. Nevertheless, in view of the great economic importance of the eel, it is obviously desirable to try to raise the yield still further. This may be done, for instance, by legal measures to regulate the catch, or by increasing the rate at which the population is recruited. This latter method is only possible, however, by increasing the number of elvers migrating from the North Sea into the lake, and our efforts to bring this about are the subject of the present paper.

As has already been mentioned, Lake Yssel is the former Zuyder Zee, and is separated from the Dutch Wadden Zee (part of the North Sea) by a large dike, a so-called "Afsluitdijk" (i.e., "enclosing dike"). The fresh water flowing into the lake is discharged into the Wadden Zee at both ends of the dike, near Den Oever and near Kornwerderzand. At the former place there are three sets of 5 sluices, and at the latter, there are two such sets. There are also 3 locks for ships, one at Den Oever, two at Kornwerderzand. A peculiarity of the sluices is that each gate has two hatches, one behind the other, several metres apart, each of which can be moved up or down. In this way the sluice can be opened or closed.

Now the only passages by which elvers could migrate into Lake Yssel are the sluices and locks through the dike. At first the elvers were allowed to pass by simply opening all the sluices, when the water levels were the same. The disadvantage of this method was that very much salt water entered the lake, and as the aim was to get the lake as fresh as possible, the method had to be abandoned.

The late biologist J. J. ter Pelkwijk then developed a method which consisted of the alternate opening of the sluice hatches several times a night, and this method is still in use. First the outer hatches are opened, the elvers swim into the sluices and assemble in front of the inner hatches. Then after two hours the outer hatches are closed and the inner hatches opened for about a quarter of an hour, to allow the elvers in the sluices to enter the lake. After this, the inner hatches are closed and the outer hatches are opened again for two hours. By this method the elvers are passed in the same way as locks are used for a ship. This method is working very well, as is proved by the still large catches of eels in the lake, about 4,000,000 kg. a year.

An attempt to learn more about the factors influencing the inward migration of elvers was made by van Heusden (1943), who studied the reactions of elvers in laboratory tests. The desirability of further investigations nevertheless remained, and I was charged with their execution.

It must be emphasized that the purpose of my studies was purely practical, viz., to develop a method of attracting a larger number of elvers out of the North Sea into the Wadden Zee and subsequently into Lake Yssel. It was therefore necessary to discover the factors which influenced the migrations of the elvers *at sea*. Accordingly the migration from the sea to fresh water and in fresh water will not be dealt with in this paper.

During my investigations I received much help from several persons, to whom I wish to express my gratitude:— Ir. H. A. M. van Erp, Inspector of Fisheries; Mr. Ch. Gilis, Expert of the Belgian Government Institute of Fisheries; Dr. P. Groen, Oceanographer of the Royal Dutch Meteorological Institute; Dr. B. Havinga, Director of the Government Institute for Fishery Investigations; J. H. Jones, M.I.C.E., M.I.M.E., Chief Engineer of the Ministry of Finance, Works and Public Buildings of Northern Ireland; F. T. K. Pentelow, Chief Inspector of Salmon Fisheries in England; H. Postma, Oceanographer of the Zoological Station at Den Helder; Dr. J. Verwey, Director of the Zoological Station at Den Helder, and A. Volker, Chief Engineer of the Government Board of Zuyder Zee Works.

I should also like to thank the following gentlemen for their assistance in fishing elvers on many days and nights:— Messrs. P. van Gorkom, J. Mennema, J. Pijl, J. F. de Veen, M. Weenink, A. J. van Tooren. Mr. de Veen also gave me much help in both observing and calculating.

Finally, I should like to express my thanks to Prof. Dr. G. P. Baerends and Dr. B. Havinga for having read and corrected my manuscript.

Records and methods.

The data studied came from two sources. The first is the statistical records from the Afsluitdijk, the River Bann, and the River Severn, and the second is my own observations.

Despite much effort, we were unable to obtain data on elver migration from other parts of Europe.

1) Afsluitdijk. As has already been mentioned, the Afsluitdijk sluices are used as elver locks during the migration season from March to May, by passing the elvers every two hours from the sea into the lake. To estimate the numbers migrating, hauls with a dip-net of 1 m^2. were made from the bottom to the water surface in the westernmost sluice of the middle set. It was situated 20·5 m. from the inner hatch, and 1·5 m. from nearest side of the sluice.

A haul was made on each occasion just before the elvers were passed through the sluices, so that the hauls were at two-hour intervals. The elvers caught were counted and the number recorded. It is assumed that a fresh group of elvers was always caught each time, because after each dip the elvers were passed through the sluices. This procedure was carried out at Den Oever from 1938 to the present time, the only break occurring in 1945, when no hauls could be made owing to the war.

A dip-net like that at Den Oever was installed at Kornwerderzand in 1948. This was located in the westernmost sluice of the eastern set, at a distance of 19·5 m. from the inner hatch and 1·5 m. from the nearest side. At Kornwerderzand great quantities of elvers are caught every year in the adjacent locks by the Fisheries Inspectorate, for transportation to inland waters, and these catches may be compared with those of the dip-net.

It was very soon evident that no constant relation existed between dip-net catches and Fisheries Inspectorate catches. The catches for short periods in a season do not tally, and the total catches for the season also differ very much. This discrepancy is only explicable on the assumption that the intensity of migration is not connected with one—or both—of the catch series. This matter is now being studied but no definite reason has so far been found. However, the dip-net data have the great advantage that the catches were made regularly, while the commercial catches were not only very irregular, but were made with different fishing intensities, and are thus likely to be less useful. We shall therefore prefer the dip-net data for our attempts to correlate different factors or combinations of factors and the migrations of the elvers at sea.

2) River Bann. In this river, which flows through Northern Ireland towards the Atlantic Ocean, elvers have been trapped and transported to inland waters from 1932 to April 1948, as has been described by Menzies (1936) and Frost (1950).

Thanks to the assistance of Mr. J. H. Jones, I have received the records of elver transportation covering the years 1936 to 1948. The records for the years 1932 to 1935 are not entirely reliable.

We must assume that the majority of the elvers reaching the Bann weir were trapped. However, it is fairly certain in my opinion that some elvers managed to pass through the lock, and in this way escaped recording. This would explain the statement by Frost (1950) that

she observed elvers swimming in the river when transportations were being made.

In addition to the elver records I also received records of the daily water discharge of the River Bann in cubic feet per minute.

3) River Severn. This well known river flows into the Bristol Channel. Elvers migrating upstream were caught for a long time near Epney, a village in the vicinity of Gloucester. They were stored there and afterwards distributed, mainly to Germany, but also to other European countries. During the second world-war the English Fisheries Inspectorate took over the storage installation.

The elvers were caught with scoops of linen mesh, placed in the river with the opening facing downstream. The elvers assemble in the scoops and can then easily be landed. It is obvious that the quantities caught do not represent the total quantity of elvers migrating upstream, but are heavily influenced by several factors, e.g., the price paid for the elvers.

Catch records have been published by Röhler (1939); those for more recent years were communicated to me by Mr. F. T. K. Pentelow.

Own observations.

To obtain information about the factors influencing the migration of elvers in the sea, I decided it would be best to begin by studying their behaviour in nature. This might yield clues which would suggest more detailed laboratory work, if wanted.

However, the study of elvers in nature has one great disadvantage, namely, that data obtained are mainly indirect: it is practically impossible to study the movements of the elvers in the sea by direct visual observation. The only available method is to draw conclusions from the catches made. Despite this drawback, it was decided to collect data on catches so that an attempt could be made to discover at least the most important factors. In the first two seasons a ship belonging to the Fisheries Inspectorate was used; it was in great demand, however, for inspection work, so that no regular observations could be made. During the last three seasons the "Max Weber," owned by the Zoological Station at Den Helder, was kindly put at our disposal, and in 1950 the fishery research vessel "Antoni van Leeuwenhoek" was also employed.

Our material was obtained by fishing funnel-shaped nets—a kind of plankton net—in the tidal streams from an anchored ship. The elvers caught must have been borne by the flow into the nets. Two nets were used simultaneously—except in 1946, when only one net was used—one at the bottom, and one near the water surface. The wire warp used for the surface net was attached to a spar projecting horizontally from the stem of the ship; the warp for the bottom net was secured to the anchor. The mouth of the net was 1 m^2. in area, circular in the surface net, rectangular in the bottom net, with sides of 141 and 71 cm. The nets first used were of woven hemp, and later on of woven flax, with a mesh surface of about $2^1/_4$ mm^2.

The length of the nets varied somewhat. At first hemp nets of 3 m. length were used; in the fourth season the flax nets were 6 m. long and in the last season about 12½ m. long. I am convinced that the nets were long enough in relation to the speed of the streams to ensure proper filtration. The hemp was smoother than the flax, so that at first short nets were sufficient. However, the possibility existed of the nets becoming dirty and impermeable, so that I finally decided to change over to nets of about 12½ m. length. A flap prevented the elvers from swimming out of the net once they had entered it.

Observations and tests showed that elvers did not try to escape while they were in plenty of water; they passed through the meshes only when the nets were hauled and the cod-end was out of the water, and when there were many jelly-fish (*Pleurobrachia*) present.

The "Max Weber" was not equipped to withstand much bad weather and we were accordingly obliged to anchor only at such places from which we could easily return to harbour. As a result we could fish at only a few places in the Wadden Zee. This was not a great disadvantage, however, for I decided it would be better to get a series of data from one position than to get data from several places, which might be difficult to interpret. It would certainly have been best to get simultaneous data from several places, but no ships were available, so that this was beyond our resources.

During the cruises water samples were taken regularly for temperature and salinity determination.

The question of using stationary gear was considered, but the idea was abandoned, on account of the fact that bad weather would have made it impossible to approach these nets at the desired time. Moreover, it is probable that heavy seas would have destroyed the nets.

Migration intensity.

The best idea of the variation in strength of the elver migration from year to year is furnished by the Bann data (Table 1b). It can be seen that the catches decreased regularly over the period considered, as was also the case at Den Oever and in the Severn (Tables 1a and 1c).

To show this decline more clearly and to minimize the influence of local factors, 3-year running means were calculated for each of the three series (Table 1). These figures indicate that the decline is fairly regular. The average catch for 1945, '46, and '47 in the Bann is 31 % less than that for 1936, '37, and '38, which is a very considerable difference.

We do not know the cause of the decline. It is possible that size of the eel population alternately rises and falls as is the case with many other animal populations. This would agree with a paper by Schnakenbeck (1950), in which he stated that the number of small eels in the Elbe estuary (which is of course dependent on the number of elvers reaching the estuary) changes very much. In 1929 small eels were very numerous. From 1929 to 1932 the number

Table 1. Yearly catches of elvers in three different localities.

a. Den Oever.

Year	Catch in numbers of fish	3-year running mean
1938	7806	—
1939	26028	12902
1940	4873	12134
1941	5502	5269
1942	5433	5770
1943	6375	9716
1944	16340	8717
1945	—	—
1946	2436	6780
1947	1564	1832
1948	1495	1702
1949	2046	1929
1950	2247	—

b. River Bann.

Year	Catch in lb.	3-year running mean
1936	16215	—
1937	19890	17915
1938	17640	17235
1939	14175	16923
1940	18955	18243
1941	21600	18633
1942	15345	17010
1943	14085	13605
1944	11385	12406
1945	11748	12665
1946	14861	12423
1947	10668	—

c. River Severn.

Year	Catch in 1/2 kg.	3-year running mean
1908	344	—
1909	1633	—
1910	3396	—
1911	3765	3212
1912	2476	3375
1913	3885	3319
1914	3596	—
1924	678	—
1925	933	—
1926	1531	—
1927	2400	—
1928	4092	3287
1929	3369	3786
1930	3897	3840
1931	4254	4093
1932	4128	3718
1933	2773	3239
1934	2815	3098
1935	3707	3411
1936	3711	3765
1937	3876	4033
1938	4512	4800
1939	6012	—
1943	1042	—
1944	999	1227
1945	1639	1383
1946	1510	1296
1947	740	841
1948	274	349
1949	32	—

1 lb. = 0·454 kg. = about 1400 elvers.

decreased, but afterwards increased till 1935, after which they steadily decreased again; no further increase was mentioned.

A second possible cause is the steady increase in the eel fishery in all countries in which this species occurs. There is no doubt that as a consequence of this the number of eels reaching their breeding places must also diminish, so that egg production will decrease too.

Comprehensive and reliable data on the catch of eels in all the European countries concerned are lacking. Even in Holland the quantity of eels caught in inland waters is unknown, except for Lake Yssel. For this reason it cannot be proved that eel catches increased generally, but from various remarks in fishing journals about increased

Table 2. The dates on which elvers were first noticed at Den Oever, and the temperature of the water in Marsdiep on the six preceding days.

1938			1939			1940			1941		
	Elvers	Temp. °C.		Elvers	Temp. °C.		Elvers	Temp. °C.		Elvers	Temp. °C.
6·III.	—	5·1	22·II.	—	4·1	29·III.	—	4·4	14·III.	—	3·9
	—	5·5		—	4·1		—	4·8		—	3·9
	—	5·6		—	4·5		—	4·6		—	4·0
	—	5·8		—	4·5		—	5·4		—	4·2
	—	6·1		—	4·6		—	5·8		—	4·1
	—	6·2		—	4·6		—	5·6		—	4·2
12·III.	23	6·0	28·II.	43	4·4	4·IV.	83	5·8	20·III.	5	4·7
	1942			1943			1944			1946	
6·IV.	—	4·7	27·II.	—	5·1	15·III.	—	4·1	5·II.	—	4·2
	—	5·4		—	5·2		—	4·3		—	4·3
	—	5·3		—	5·5		—	4·6		—	4·5
	—	5·5		—	5·7		—	4·7		—	4·8
	—	5·1		—	5·9		—	4·8		—	4·7
	—	5·4		—	5·0		—	4·7		—	4·3
12·IV.	2	6·0	5·III.	11	5·4	21·III.	3	4·7	11·II.	3	4·7
	1947			1948			1949			1950	
5·IV.	—	4·6	11·III.	—	4·5	11·II.	—	4·1	3·III.	—	4·7
	—	4·4		—	4·8		—	4·4		—	5·1
	—	4·4		—	5·0		—	4·3		—	5·3
	—	3·7		—	5·1		—	4·7		—	5·3
	—	4·4		—	5·3		—	4·9		—	5·0
	—	4·2		—	4·3		—	4·9		—	5·3
11·IV.	5	4·8	17·III.	3	5·5	17·II.	6	4·7	9·III.	16	5·6

fishing intensity and improvement of methods, we may assume with fair certainty that this is so.

Influence of wind and temperature.

Our investigations provide no evidence that wind exerts any influence upon migration at sea.

In the vicinity of sluices or other freshwater outlets there seems to be a relation between the wind and the dispersion of the elvers. This matter is being investigated and will not be discussed at present.

With regard to temperature, we may assume that this is a factor starting or delaying migration. This may be studied by considering the temperatures on the days on which the elvers were noticed for the first time.

Menzies (1936) states that low air temperatures in the Bann check elver movement into the trap. It is possible, however, that this is due to local effects and it does not follow that this applies to elver migration in the sea too.

Table 3. Number of elvers caught at Den Oever and the water temperature at Marsdiep, 1949.

	Elvers	Temp. °C.		Elvers	Temp. °C.		Elvers	Temp. °C.		Elvers	Temp. °C.
17·II.	6	4·7	27·II.	—	5·4	8·III.	0	2·0	17·III.	1	4·1
	9	4·3		—	5·0		0	2·1		8	4·3
	5	5·0	1·III.	—	4·5	10·III.	0	2·3		3	4·2
20·II.	8	4·6		4	4·2		2	3·1	20·III	6	4·1
	4	5·2		2	3·8		0	3·2		13	4·5
	11	5·0		0	3·8		0	4·4		19	4·2
	5	5·5		10	2·4		3	4·3		31	4·9
	2	5·4		6	2·2		10	4·3		8	5·1
	7	5·5	7·III.	1	2·5	16·III.	12	4·4	25·III.	53	5·3
26·II.	5	5·4									

Table 2 enables the dates on which elvers were first caught at Den Oever to be compared with the corresponding water temperatures near Den Helder (the nearest place for which temperature data were available). We must recognize, however, that fishing with the dip-net did not begin until there were elvers present, and until there were no objections from the Board of Zuyder Zee Works, e.g., with regard to the water discharge. That is to say, fishing never began early, but only either late or in time. Bearing this in mind, we can perceive in the table a fairly close relation between water temperature and the date of arrival of the elvers. Below a temperature of about 4·5°C. elvers do not usually arrive. We are inclined to believe that the elvers require this temperature at least, before they begin migrating at sea. This is demonstrated nicely by the following instance. In 1949, the elver migration began early. Later on the onset of very cold weather caused the water temperature to fall suddenly, immediately after which the elver migration ceased entirely. Although elvers were observed in the sluice when the temperature was 2·2°C., the migration itself was interrupted. An uninterrupted elver migration did not begin again until the temperature rose to about 4·5°C.

Van Heusden (1943) was also aware of this. He stated that no elvers appeared at a water temperature of 3°C., and that, in his opinion, the main migration occurred at temperatures between 6° and 11°C. He assumed that this was a direct effect, i.e., that elvers wanted to migrate only when the temperature was between these two limits and that the migration urge disappeared when the temperature was lower than 6° or higher than 11°C.

A similar relation can be found, of course, for every animal which migrates in a certain season, but this does not imply that the effect is direct. It is much more probable that it is indirect. If we compare, for instance, temperature and catch for the River Bann (Table 4), we see that the main elver migration takes place between 7° and 10°C.; that is, between temperature limits other than those operating at Den Oever. These temperature data were collected at a position 54°57′N., 5°28′W.,

Table 4. 5-day averages of elver catches in the River Bann during the period 1936-1946, and 5-day averages of sea water temperature in the North Channel.

Elvers lb.	Temp. °C.	Elvers lb.	Temp. °C.	Elvers lb.	Temp. °C.	Elvers lb.	Temp. °C.
0	6·9	247	7·5	324	8·2	93	9·3
67	6·9	373	7·6	204	8·6	91	9·6
80	6·9	319	7·7	246	8·9	142	9·8
209	7·0	321	8·1	204	9·0	82	9·9
186	7·1						

about 100 km. from the Bann estuary. According to the monthly synoptic charts published by the Fisheries Laboratory at Lowestoft, in a distance of this order the temperature change in the sea water is considerably less than 1°C., so that we may correlate these temperatures with the Bann catches.

It is logical to assume that once the migration has begun it will continue, so long as the temperature is above the minimum value. In that case the quantities of elvers arriving will be determined primarily by the number of elvers in the sea. The coincidence of greatest intensity of migration with certain water temperatures may be due to accident, and cannot be regarded as significant. Moreover, we must suppose that the end of the migration will be determined by the absence of elvers in the sea and not by water temperature.

This view is supported by the fact that in late summer every year (in July and even August) some migrating elvers can still be observed in the locks and sluices of the Afsluitdijk, and this migration is not apparently checked by high temperatures.

The data collected during our work at sea also support this view; no correlation between migration and water temperature can be found from them.

Another possibility is that it is temperature differences which act as guiding factors. It is sometimes thought that temperature differences are responsible for the elver migration from the North Sea into the Dutch Wadden Zee; the warmer water of the Wadden Zee should "attract" the elvers away from the cold North Sea. That this opinion cannot be true is evidenced by figures published by P o s t m a and V e r w e y (1950) for the water temperature at a certain point in the North Sea, at the entrance to the Wadden Zee, and at a point in the Wadden Zee. They show that at exactly the time when migration is most intense (March—April) the average temperatures are the same at all those places, so that there can be no attraction by warmer water in the Wadden Zee.

Influence of light.

It is commonly known that light exerts a great influence upon the conduct of migrating elvers. An interesting proof that in the dark elvers prefer to swim near the surface has been given by v a n H e u s d e n

Table 5. Elver catches expressed as percentages of the nightly total catch at different times of the night at Den Oever.
(Amsterdam mean time).

1938		1939				1940	
hrs.	%	hrs.	%	hrs.	%	hrs.	%
1910	4·8	1900	5·1	1800	3·3	1900	5·4
2110	13·5	2100	14·6	2000	11·0	2100	14·3
2330	22·5	2300	17·8	2200	23·0	2300	22·5
0150	28·0	0100	24·3	2400	25·1	0100	24·7
0410	26·3	0300	23·4	0200	31·3	0300	23·3
0610	10·3	0500	14·7	0400	3·3	0500	10·3

	1941	1942	1943				1944	
hrs.	%	%	hrs.	%	hrs.	%	hrs.	%
1820	5·1	1·6	1920	4·3	1820	1·6	1920	8·4
2020	8·3	10·4	2120	13·0	2020	11·7	2120	20·6
2220	16·9	26·8	2320	24·2	2220	25·8	2320	21·7
0020	25·4	31·2	0120	22·0	0020	27·4	0120	20·0
0220	25·5	19·7	0320	24·6	0220	20·3	0320	18·5
0420	16·2	10·2	0520	12·6	0420	12·6	0520	11·1

1944		1946	1947	1948	1949
hrs.	%	hrs.	%	%	%
1820	1·6	1920	7·6	2·5	9·1	2·9
2020	9·3	2120	17·4	10·3	16·8	12·8
2220	18·8	2320	28·4	24·6	23·4	22·0
0020	24·9	0120	25·2	24·0	26·0	29·7
0220	24·0	0320	18·5	27·4	17·6	28·3
0420	21·4	0520	10·5	6·8	8·6	4·1

(1943), who kept elvers in an aquarium in a room that was completely blacked out. Van Heusden turned the light on and off an hour earlier each day, so that at last a situation was reached at which the room was light at night, and dark by day. In these conditions the elvers swam only in the dark hours, that is, during the day, and kept themselves dug in the sand during the night when the lights were burning; they thus behaved in complete contrast with their congeners not kept in this room.

A good opportunity to study the relation between light intensity and migration urge is provided by the numerous dip-net data for Den Oever from 1938 to 1950. For this purpose these are used for comparison with each other and not for quantitative studies, and in this respect they may be regarded as fully trustworthy.

For this comparison those nights were selected on which at least 20 elvers were caught. The catch of each seperate haul is expressed as a percentage of the total catch (of 6 hauls at 2-hour intervals) for each night.

The hauls were made at the same hour each night. By summing the respective percentages, we have computed the average percentage

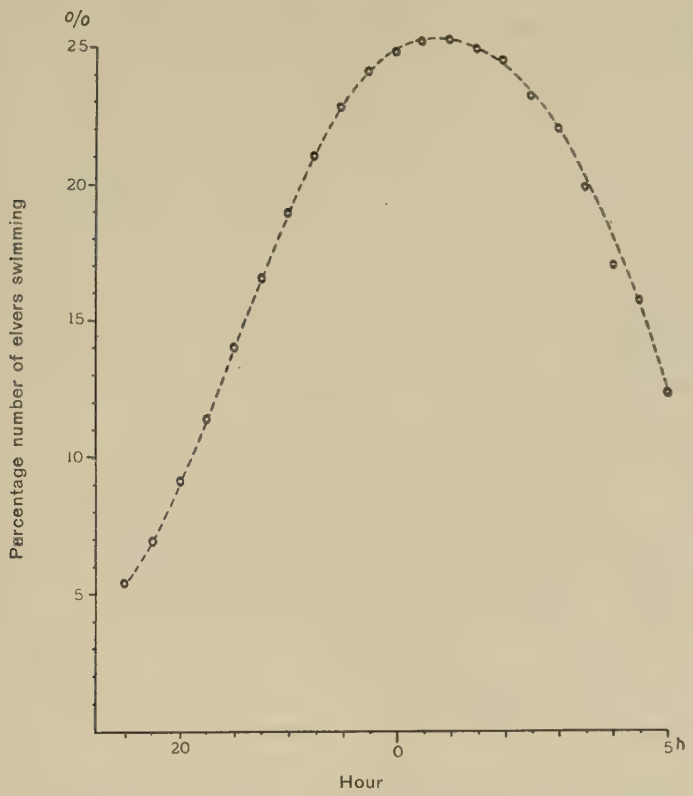

Figure 1. Average course of the nightly activity of the elvers at Den Oever, 1938—1949.

catches for various times, and so shown the average course followed by the elver activity during the night (Table 5). A graph was drawn for each season, and the values read off at the intersections of the curves with the ordinates at half-hour intervals.

The averages so obtained for each set of these values is shown by the curve in Figure 1. This graph represents the average nightly swimming activity of the elvers. Similar graphs have been drawn for 1938 by ter Pelkwijk and for 1942 by van Heusden (1943).

Figure 1 demonstrates that swimming activity is greatest during the night. Furthermore, it may be seen that activity does not immediately become maximal at the beginning of the night but increases gradually, i.e., more and more elvers swim as the night advances. This may be explained by assuming that the migration urge also increases gradually during darkness, and that the elvers begin swimming after the urge has reached a certain strength. As this intensity will be attained at different times in different individuals—just as with many other species—it is obvious that the number of elvers swimming will gradually increase during the course of time.

During the day almost no elvers are recorded, as our graph indicates. It must be concluded that the elvers are not then entirely absent from the vicinity of the sluices, but are dug into the sand on the bottom, as described by van Heusden (1943), or remain stationary in deeper water, as was found in the following way. At a distance of about 150 m. from the sluices there is a deep pit in the sea bottom. When dip-netting here at about noon on 6. April 1951 at a depth of 5 m., we caught 1, 1, 1, 2, and 0 elvers. Repeating the hauls at a depth of 20 m. immediately afterwards, we caught 40, 30, 59, 54, and 43 elvers. There was no difference in temperature, and a difference of 1 $^0/_{00}$ in chlorinity between the two depths. For the most part they do not migrate, at this time, in contrast with their behaviour in the open sea, which will be discussed later on.

A question which may be put is whether the curve (Figure 1) retains the same shape throughout the migration season. This has been investigated by drawing four similar graphs for four subsequent fortnights (Figure 2). Not enough data were available for a fifth period.

We again observe the fact that elvers begin swimming about sunset, i.e., the migration urge accumulates during the day and activates the elvers when it is getting dark. Extrapolation suggests that elvers begin to swim about $1^1/_2$ hours before sunset. The number of elvers swimming gradually increases up to a certain point, after which it decreases. We cannot help thinking that the number at this point is determined by the beginning of astronomical dusk, i.e., when the sun is 18° below the horizon.

The peaks of the earlier curves are distinctly flatter than the later ones. This can be explained by the fact that with the first curves the nights are longer. There will therefore be more time for swimming —when the greatest intensity of migration is attained—than later on in the season. A peculiar phenomenon is that in later periods maximal elver activity is reached at an earlier hour than in the beginning of the season. This may be understood by considering that in the later period water temperature is higher than in the earlier. As we may suppose that temperature influences the sensibility to light, as is the case with other animals, this would mean that in the later periods elvers would be more sensible than in the earlier, and would thus react more quickly.

As regards the effect of moonlight on elver migration, it may be that moonlight exerts no influence at all, or that it completely stops the elvers from swimming. A third possibility is that the effect of moonlight is delayed, so that the migration urge accumulates until the elvers eventually swim.

To investigate this, the average catches on days of full and new moon were calculated from the Bann data (Table 6). From these figures we cannot conclude that elvers migrate less actively at full than at new moon, whence it would seem that our second supposition does not hold good. Whether the first and third suppositions are true I cannot decide.

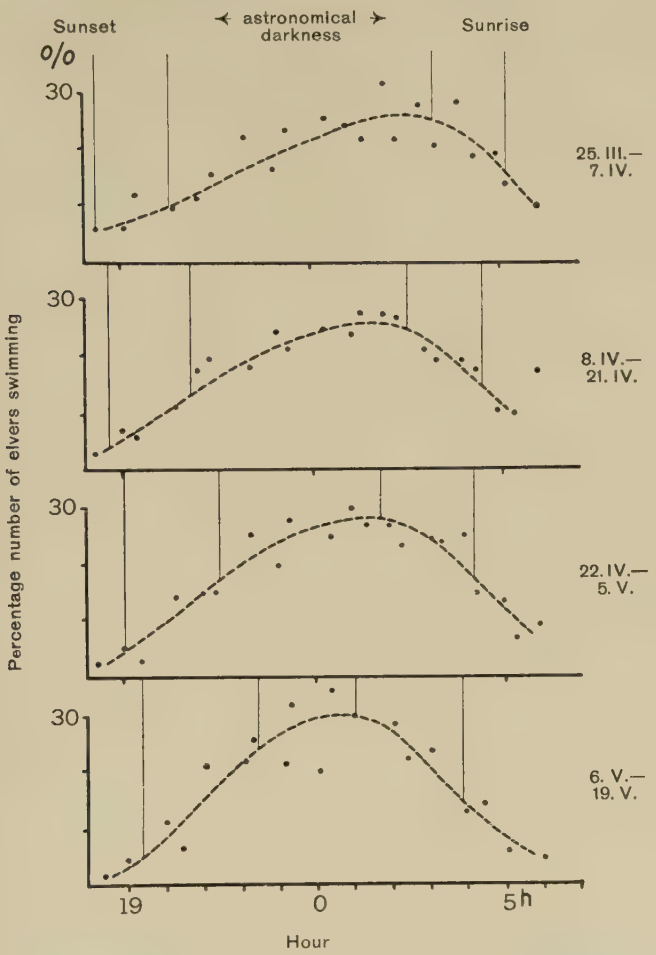

Figure 2. The average course of the nightly activity of the elvers at Den Oever in four successive fortnights, 1938—1949.

Table 6. Average daily catch of elvers (lb.) in the River Bann at full and new moon.

Phase of the moon		Daily catch made at:
Full	New	
319	268	two days before
349	329	one day before
316	300	the day itself
320	251	one day after
316	225	two days after
Total		
1620	1373	

It is often alleged that an artificial light attracts migrating elvers, and elver fishermen make use of this idea to improve their catches. However, Eichelbaum (1923—'30) could not confirm that this is the case.

Preliminary observations have given the impression that elvers are attracted by light within a certain intensity range and are repelled when the intensity is beyond this range. Presumably also other factors, operating in the past or present, may effect the reactions of elvers to various intensities and quantities of light.

The influence of the saltness of the water.

Verwey (1949) supposed that elvers find their way from the sea into fresh water by indulging an innate preference for certain conditions of milieu, and it is commonly supposed (see van Heusden, 1943) that the most important of them is the proportion of fresh water present, as indicated by the salinity.

It is unfortunate that the Bann data are of little help in studying this matter, for the following reason. The Bann weir is divided into three parts, the southern part with the sluice gates, the middle part with the fish cribs, and the northern part with a single weir (see Menzies, 1936). Normally, water is discharged through the middle part, so that the fresh water is discharged directly towards the estuary. As the river rises, first the northern part and then the southern part begin to discharge too. Moreover, the situation is further complicated, because the gates of the sluices can be drawn. The fresh water passing the northern and southern parts flows in a direction oblique to the estuary. It is certain, so a Chief Engineer of Rijkswaterstaat assured me, that these oblique movements drive great quantities of fast flowing water into the banks of the estuary in front of the weir. This does no harm because

Table 7. Average catch of elvers and quantity of water discharged at the first weir in the River Bann.

Elver catches in pounds/day; water discharge in 10^3foot^3/min./day.

1942	Elvers	Discharge	1945	Elvers	Discharge
2.—6. April	36	124	30. May—3. June	7	132
7.—11. „	36	338	4.—8. June	40	266
12.—16. „	0	460	9.—13. „	0	345
17.—21. „	441	121	14.—18. „	0	189
22.—26. „	405	47	19.—23. „	77	61
1943			1947		
30. Apr.—4. May	144	73	18.—22. April	132	40
5.—9. May	144	39	23.—27. „	28	281
9.—14. „	0	402	28. Apr.—2. May	0	308
15.—19. „	162	101	3.—7. May	0	279
20.—24. „	297	54	8.—12. „	171	139
			13.—17. „	627	96

Table 8. Chlorinity of the water at surface and bottom at various places on days during a certain period on which no water was discharged at Den Oever.

A. At Visjagersgaatje, 17. April to 8. May 1948.

Date April 1948	Time	Chlorinity (Cl ‰) Surface	Bottom	Date April 1948	Time	Chlorinity (Cl ‰) Surface	Bottom
18.	0000	14·56	14·54	19.	1300	15·20	15·20
	0100	14·71	14·71		1400	15·06	15·09
	0200	14·77	14·77		1500	15·15	15·14
	0300	14·21	14·72		1600	15·06	15·21
	0400	14·11	14·66		1700	15·19	15·45
	0500	14·11	14·58		1800	15·06	15·18
	0600	14·60	14·76		1900	15·30	15·30
	0700	14·79	14·91		2010	15·56	15·55
	0800	15·18	15·24		2100	15·57	15·57
	0900	15·07	15·31		2200	15·65	15·60
	1000	15·20	15·24		2300	15·64	15·65
	1100	14·56	14·57		2400	15·60	15·60
	1200	14·55	14·58	20.	0100	15·66	15·65
	1300	14·67	14·95		0200	15·52	15·48
	1400	14·76	15·26		0300	15·26	15·26
	1500	14·68	15·30		0400	15·28	15·31
	1600	14·57	15·16		0500	15·25	15·30
	1700	14·63	14·77		0600	15·25	15·25
	1800	14·76	14·77		0710	15·36	15·46
	1900	15·17	15·13		0800	15·55	15·56
	2000	15·47	15·46		0900	15·55	15·57
	2100	15·56	15·52		1000	15·65	15·60
	2200	15·56	15·56		1100	15·65	15·65
	2325	15·47	15·57		1200	15·65	15·56
19.	0025	15·34	15·36		1300	15·64	15·58
	0100	14·95	14·97		1400	15·56	15·56
	1200	15·54	15·56		1500	15·46	15·39

the banks of the Bann estuary are rocky, but this would not be the case in Holland, for instance; such violent oblique currents would destroy the river banks. It is therefore clear that even close to the banks of the Bann the flow of water is sometimes so strong that the tiny elvers can find no shelter there and are very much hindered or completely prevented from migrating upstream. Hence it can be understood why with high rates of discharge (Table 7) few or no elvers were recorded. This is not because no elvers were present at the moment, but because they were unable to pass certain particularly turbulent parts of the river. It seems to me improbable that the elvers would wait indefinitely for a suitable moment to pass; they may have done so for a while, but under the influence of their steadily accumulating migration urge, they would probably try again and again until they became exhausted and were smashed against the rocks and killed. We may also expect that this happened to some extent with lower rates of discharge, with for

Table 8, contd. **B. At Visjagersgaatje, 24. March to 21. April 1949.**

Date March 1949	Time	Chlorinity (Cl ‰) Surface	Bottom	Date April 1949	Time	Chlorinity (Cl ‰) Surface	Bottom
31.	0020	15·23		20.	0045	17·26	
	0120	15·27			0310	17·20	
	0220	15·33			0420	17·20	
	0320	15·31			0800	17·27	
	0400	15·22			0925	17·26	
	0450	15·25	15·26[5]		1030	17·26	
	0550	15·22			1310	17·41	
	0635	15·22			1350		17·35
	0735	15·22			1505	17·23	
	0840	15·28	15·27		1610	17·25	
	0940	15·23			1740	17·28	
	1040	15·26			1910	17·36	
	1140	15·34			2030	17·38	
	1240	15·34			2135		17·36[5]
	1340	15·34			2140	17·36	
	1440	15·32			2245	17·33	
	1540	15·26			2345	17·24	
	1650	?	15·26[5]	21.	0210	17·41	17·33[5]
	1735	15·35					
	1845	15·30					
	1950	15·31					
	2040	15·34	15·36[5]				
	2235	15·39					
	2335	15·34					

instance only the weir working. It would seem unjust to correlate the quantity of water discharged with the numbers of elvers recorded at the Bann weir, because each state of water discharge is associated with its peculiar hydrographical conditions below the weir system, depending on the tides and wind direction.

As regards the Den Oever data, we have to reckon with the fact that we do not know the relation between the dip-net catches and the total number of elvers migrating. Hence no direct comparison between catches and water discharge can be made, but the problem can be approached in another way.

It is commonly assumed that elvers arrive at Den Oever when fresh water is discharged. When, however, this does not occur, the salinity differences in the sea water rapidly disappear. According to our observations, it takes only a few days for the water to become homogeneous over great stretches, under the influence of the wind, the differences in velocity in the tidal streams through the gullies and over the flats, etc. This effect is clearly shown by the data in Tables 8A, B, and C. Our ship being stationary, the tidal streams transported great masses of water past the ship. Accordingly a series of identical salinities indicates a large homogeneous water mass. The situation may then be such that as we go from Den Helder to Den Oever, the salinity remains

Table 8, contd. **C. At Wierbalg and Zwin, 22. March to 17. April 1950.**

Wierbalg				Zwin			
Date March 1950	Time	Chlorinity (Cl ‰) Surface	Bottom	Date April 1950	Time	Chlorinity (Cl ‰) Surface	Bottom
28.	0240		13·71	14.	0110	17·99	
	0300	13·68			0140		18·02
	0400	13·69			0220	18·00	
	0500	13·61			0320	17·94	
	0605	13·35			0420	17·94	
	0800		13·71		0530	18·01	
	1000	13·61			0720		18·01
	1100	13·77			0830	18·02	
	1205		13·78		0930	18·01	
	1835	13·83			1030	18·05	
	2110		13·91		1050		17·93
	2305	13·77			1830	17·94	17·96
29.	0005	13·82			1935	17·95	
	0225		13·82		2035	17·96	
	0600	13·88			2150	17·98	
	0700	13·79			2245	17·92	
	0800	13·79			2345	17·93	
	0900	13·67		15.	0045	17·93	
	1000	13·71	13·92		0145	17·96	
	1100	13·70			0545	17·96	17·93
	1200	13·78					
	1310	13·90					
	1440	13·88					

the same for some distance, then suddenly falls, after which it again remains the same at the lower value, until it suddenly falls again (P o s t m a[1])). A gale may cause these salinity "steps" to disappear, so that the salinity is then constant over the whole region. This condition was found to exist after the severe gale of 9. and 10. April 1950, after which the salinity in the Wadden Zee was as high as that in the North Sea, and this situation must have lasted until the first discharge of fresh water on 17. April 1950 (see Table 9).

Table 10 shows that long periods of no discharge occur and we may expect that during these periods there were no salinity differences over considerable distances. Nevertheless the elver migration at Den Oever continued normally, as, for instance, was the case in 1942 (Table 11).

It might be suggested that the appearance of normality at these periods is nothing more than a fall in an otherwise abnormally intense migration, but in this connexion it may be remarked that since it has been shown that many elvers were able to reach the Den Oever sluices without the guidance of salinity differences it may be assumed that most elvers would have been able to do the same. Moreover, if we consider our data on catches and salinity in the Wadden Zee, we find no suggestion of a correlation between salinity changes and migration.

[1]) Private communication.

Table 9. Chlorinity of the Wadden Zee water between Den Helder and Den Oever on 13. April 1950, on the p. m. high tide.

The samples were taken from the "Antonie van Leeuwenhoek".

Time hrs.	Chlorinity (Cl ‰) Surface	Bottom	
1418	18·00	18·01	Black buoy, Den Helder
	—	18·03	Red 1, Malzwin.
	18·05	18·04	Red 2
	18·05	18·05	Red 3
	18·06	18·11	Red 4
	18·10	18·11	Red 5
	18·07	18·13	Red 6
	18·13	18·14	Red 7
	18·13	18·20	Red 1, Wierbalg.
	18·18	18·20	Red 2
	18·17	18·19	Red 3
	18·21	18·16	Red 4
	18·12	18·15	Red 5
	18·12	18·13	Red 6
1622	18·02	18·12	Red 7, Wierbalg, Den Oever

For these reasons we must reject the idea of any relation between intensity of migration and salinity of the sea water. This does not apply, however, to the vicinity of fresh water outlets. Since elvers congregate in river mouths or in front of sluices, lock gates, etc., we must certainly expect that in these surroundings fresh water plays a rôle in the elver orientation.

Influence of tidal streams.

The opinion has often been expressed that elver behaviour is probably influenced by tidal movements; elvers may tend to travel especially on the spring flood (Fischer und Lübbert, 1911; Lübbert und Fischer, 1911; Lübbert, 1928). In this connexion the last-named author declared "Ungeheure Mengen von Glasaalen werden durch die

Table 10. Continuous periods in which no water was discharged at Den Oever in elver seasons and in which the elver migration continued normally.

1940.	9.—21. April
	24. April—5. May
1941.	29. April—29. May
1942.	16. April—27. May
1943.	6. March—25. March
	7. April—20. April
	30. April—22. May (end of migration)
1948.	17. April—8. May (end of migration)
1949.	5. March—18. March
	24. March—21. April
1950.	22. March—17. April

Table 11. Dip-net catches at Den Oever in 1942, and quantity of fresh water discharged.

Date April	Number of elvers caught	Quantity of water discharged 10^6 m.^{3}	Date May	Number of elvers caught	Quantity of water discharged 10^6 m.^{3}	Date May	Number of elvers caught	Quantity of water discharged 10^6 m.^{3}
11.	0	24	1.	162	0	21.	24	0
12.	2[1])	0	2.	124	0	22.	14	0
13.	1	120	3.	366	0	23.	44	0
14.	16	106	4.	374	0	24.	9	0
15.	33	80	5.	181	0	25.	17	0
16.	20	34	6.	311	0	26.	17	0
17.	217	0	7.	142	0	27.	20	30
18.	98	0	8.	149	0	28.	11	28
19.	93	0	9.	136	0	29.	24	30
20.	258	0	10.	59	0	30.	31	24
21.	134	0	11.	85	0	31.	23	0
22.	107	0	12.	93	0			
23.	337	0	13.	157	0	June		
24.	143	0	14.	110	0	1.	28	34
25.	179	0	15.	130	0	2.	9	34
26.	135	0	16.	139	0	3.	5	33
27.	172	0	17.	9	0	4.	11	0
28.	44	0	18.	85	0	5.	12	0
29.	68	0	19.	77	0	6.	5[2])	0
30.	127	0	20.	56	0	7.	0	0

[1]) Beginning of the season.
[2]) End of the season.

Tidebewegung zwangsläufig in diese Aalreuse (Bristol Channel) hineingetragen", and also, "Von diesen Frühjahrsspringfluten werden nun die ... Glasaale erfasst und in den Severn hineingedrückt".

R ö h l e r (1939) also considers that this applies to the elver migration in the River Severn, and M e n z i e s (1936) states that in the River Bann the elvers migrate upstream on the spring flood.

The extensive data from the Bann permit us to investigate the validity of this concept. This has been done by computing the average catches on the days before, during, and after spring tides and of the days before, during, and after neap tides. If there is in fact a relation, we may expect the average catches of the first group at least to exceed those of the last. However, from the figures given in Table 12, it appears that the differences do not support such a view. As Table 12 is based on large numbers of data, we must draw the contrary conclusion that spring tides exert no special influence upon the elvers.

The reason why opposite opinions are held by some fisheries experts may be explained perhaps as follows:— These opinions are most strongly expressed in relation to the elver migration near Epney on the

Table 12. Average daily catch of elvers (lb.) in the River Bann during spring and neap tides.

Spring tide	Neap tide	Daily catch made at:
292	203	three days before
339	258	two days before
307[1])	280[2])	one day before
284	300	the day itself
268	320	one day after
204	331	two days after
204	304	three days after
Total		
1898	1996	

[1]) Full or new moon.
[2]) First or last quarter.

Severn. Here an up-river stream occurs only during spring tide; this flows for an hour and is followed by an out-going stream of nearly 11 hours. As the differences in water level at sea are greatest during springs, it is obvious that the speed of the out-going streams at springs will be greater than at neaps.

During my investigations I observed that when migrating into fresh water elvers are very sensitive to adverse currents. They do not allow themselves to be carried back by the flow, but immediately swim to the side where the current is less strong. In my opinion the method of fishing on the Severn is also based upon this feature; the elvers having discovered the lee afforded by the linen scoops, swim into them and remain there steadily stemming the weaker flow. Since the down-river flow is fastest at springs, it is reasonable to assume that at that time the elvers will tend to swim near the banks, and moreover are more inclined to seek the lee side of the scoops, and the catches will consequently be higher. This might be ascribed to a greater intensity of migration, which need not necessarily be the case.

Besides those at springs, the tidal streams at intermediate stages are also believed to carry elvers (Eichelbaum, 1923—'30). Van Heusden (1943) further assumed that at sea elvers make use of the flood stream for transport by swimming in the upper water layers while the stream is flowing, and keeping close to the ground or digging themselves in during the ebb stream. We may consider the validity of these opinions. During the years 1908—1914 and in 1924 and 1926 Mr. Ch. Gilis studied herring larvae; he fished both by day and by night with a fine-mesh net off the Belgian coast and in the English Channel. At the same time he also recorded the elvers caught and this information was kindly set at my disposal. If these data are arranged according to ebb and flood, 26 hauls at the surface on the flood, lasting 2240 minutes, yielded 171 elvers, i.e., 2·3 elvers per 30 minutes. For the ebb 41 hauls totalling 2275 minutes fishing gave a catch of 298 elvers, i.e., 3·9 elvers per 30 minutes. This finding is not in agreement with the opinion mentioned above.

The same conclusion can be derived from the Bann catches. Table 12 compares the average catches at springs with those at neaps. The data are used in a graph (Figure 3) showing the average catches during a whole tidal period. It may be noted that there is a slight error in the graph. The interval between two consecutive spring tides has been taken as 14 days, whereas it should be half a lunar month, i.e., 14·3 days (see S v e r d r u p, 1946).

According to the Dutch Admiralty, the "mean high water lunitidal interval" (the interval between the moon's meridian passage and the next high water) is 6 hours. This enables us to calculate the time of high water expressed in mean time on a certain day according to the moon's phase.

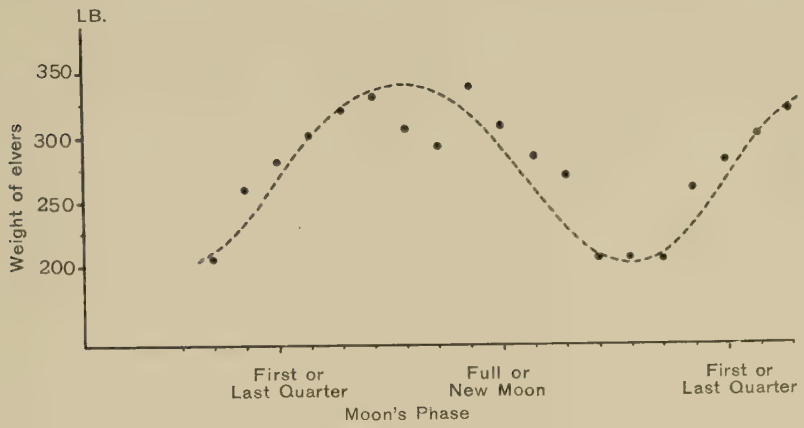

Figure 3. Showing the average daily catch of elvers in the River Bann at different phases of the moon.

Figure 3 indicates that relatively few elvers are caught in the period of about 3 days before first or last quarter, while in the period of about 3 days before full or new moon catches are relatively high. Now we may reckon that in the first period the time of high water is about 22.00 hrs. and about 16.00 hrs. in the second period. This means that in the first period the tide starts to fall early in the night, but in the second period it begins to rise at this time. Moreover, we must recognize that the falling and rising tides coincide with out-going and in-going currents in the estuary.

Let us suppose that a mass of elvers is moving towards the Bann weir. It is obvious that during a certain period (in this case the night) when the current is contrary (out-going flow) relatively fewer elvers will arrive than with a following current (in-going flow). We have already seen (page 197) that near freshwater outlets most elvers begin to swim after sunset. At that time the tide starts to rise in the period of 3 days before full and new moon, in complete contrast to the periods a week earlier or later when the tide starts falling at that time. This provides a plausible explanation of the alternately large and small

catches in the Bann; moreover, it is clear that elvers are not transported exclusively by the flood stream. If this were the case, the result would be that practically none would be caught in the periods before first and last quarter and a huge quantity in the periods before full and new moon at the Bann weir.

In the peak before full or new moon there is a distinct irregularity. I cannot explain this, though it may be the "dog-toothing" which occurs so frequently in biological data. Perhaps it is the result of several factors, which tend to bias the average catches, e.g., 1) the rate at which elvers swim, 2) the corrections to the "mean high water lunitidal interval" (these are negligible on days of full or new moon, and $1^1/_2$ hours at most on days of first or last quarter), 3) the fact that catch data have been averaged over the whole elver season (we know that in the beginning of the season maximal nightly elver activity is attained at a later hour than later in the season; the frequent occurrence of a certain seasonal period may alter the time of maximal elver activity by an hour or so. For a particular stage of the tide this means a shift of a day or more), 4) particular weather conditions, e.g., low temperatures on the elver slip, or 5) particular hydrographical conditions, connected with the outflow of the river water below the weir, which may hamper or encourage migration. As these conditions change with the height of the tide, it implies that they are in constant relation to the moon's phase, and in our figure, are emphasized by our method of summing the catch data.

A further attempt to establish a relation between elver behaviour and the tide has been made, using the data for Den Oever. If we count the number of times peaks occur in migration intensity in the 6 different 2-hour periods of the night, we may estimate the chances of peaks occurring in the same period in two subsequent nights, and for three, four, and five nights. For each category a certain value has been found for the number of times that the peak in migration intensity on subsequent nights has to occur in the same 2-hour period.

We then get:—

Peaks occur in ... subsequent nights in the same 2-hour period.	estimated	observed
1 night	213	161
2 nights	46	51
3 »	11	20
4 »	3	6
5 »	1	0

We perceive that for 2, 3, and 4 nights the observed numbers are greater than the expected. This points to the existence of some—though slight—connexion of the hour of maximum with an unknown factor, operating in the same 2-hour period of several subsequent nights. This factor therefore does not vary widely, and appears to be connected with the phase of the moon. Table 13 gives the number of times a migration peak occurs in a certain period together with the age of the moon. A

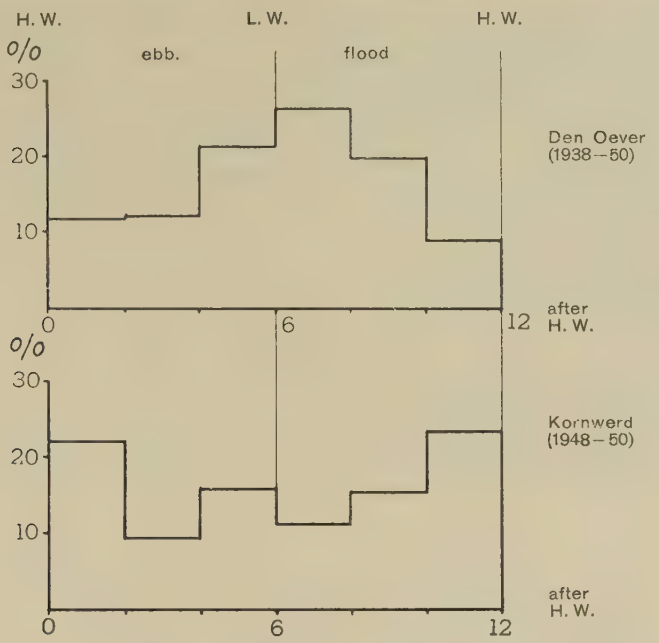

Figure 4. Showing the frequency of occurrence of peaks in nightly migration in 2-hour periods after high tide.

distinct shift of the maxima is to be seen, which suggests that this is connected with the time of moonrise, which becomes steadily later as the age of the moon increases.

As the same phenomenon occurs at both new and full moon we must conclude that it is not the moon itself which exerts an influence, but an associated factor, which would of course be the tidal movement.

To verify this, the hours between high tides and the peaks of nightly migration have been enumerated. It appears that at Den Oever the peaks mainly occur 6—8 hours after high tide, i.e., just after low tide (Figure 4). However, if we treat the Kornwerderzand data in the same way, we find that most peaks occur just after high water (Figure 4).

Table 13. The frequency of occurrence of greatest catches at different times of the night for different ages of the moon.

Time hrs.	Age of moon, days																												
	0	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	20	1	2	3	4	5	6	7	8	9
—22	1	1	1	1	3	**3**	**5**	**2**	3	1	2						1					1	**5**	1	2	1	2	2		1
— 0	2	1	2	4	1	1	2	4	**5**	**9**	**5**	2	4	1	1	1	1	1	3	3	1	2		**5**	**6**	1	4	1		
— 2	3	**7**	1	1		4	3	1	2	2	3	**5**	**7**	**6**	3	3	3	2	3	3	3	1	2	2	**3**	**7**	**3**	4	4	
— 4	**5**	**6**	3	2	5	4	3	1	1		1	4	2	5	**5**	**8**	**4**	3	2	3	3	3	1	1	1	1	3	**3**	**6**	**2**
— 6	4		1		1	1						1		1	2	**2**		**3**	**2**		1	1	3	1			1	1	2	1
	•							•							•								•						•	
	New Moon							First Quarter							Full Moon								Last Quarter						New Moon	

The only conclusion we may draw is that the correlation between elver catches and tides at the sluices of the Afsluitdijk is incidental, and caused by the coincidence of local hydrographical circumstances with the tidal movement. Possibly the streams occurring below the sluices during the ebb or the flood tide are such as to transport the bulk of the elvers towards or away from a certain set of sluices, thus biasing the catches. But in this case it would not be right to draw conclusions about the elver migration.

It may be asked why there is so much difference in the fishing at the Bann weir and at the Afsluitdijk.

The elver traps in the Bann river are situated at the head of an estuary. So the tidal streams are directed towards or away from the traps. At Den Oever and Kornwerderzand the situation is completely different. Here the tidal streams move along the freshwater outlets, i.e., the streams run perpendicularly to the axes of the sluices, while in the Bann they are in the same line. Hence it is obvious that the effects of the streams will differ in the two different sets of conditions.

Our own observations made in the Wadden Zee were collected as simultaneously as possible at the surface and the bottom of the water, as earlier described (page 190). Owing to the difference in velocity of the streams at surface and bottom these observations are not strictly comparable. As the difference is unknown, the catches do not provide a safe estimate of the relative amounts of elvers in the two water-layers. Unfortunately I did not manage to obtain accurate flow-meters for the nets.

On the other hand, although the difference in velocities is unknown their relation at a given place is practically constant, according to the experts. The bottom velocity depends on the surface velocity and the depth. We may therefore expect the relation between the quantities of elvers to be fairly constant also, provided that the elvers behave similarly in these two levels.

The complete data are not printed here, to save expense. Anyone interested may have them on application to the author.

When studying our catch data, we must remember that the records do not account for the whole quantity of elvers present at the particular moment; doubtless many elvers remained buried in the sand, or were so close to the bottom that they were not carried along by the flow and could not therefore be caught. The elvers recorded were only those swimming or floating in the water, near either surface or bottom.

The fact that our nets caught elvers certainly indicates that elvers are transported horizontally by the flow of water. We shall later see that there are also vertical movements of elvers. As these cannot be caused by the flow, they must be determined by the elvers themselves.

Before considering the question of tidal influence, we must eliminate the effects of the day-night rhythm. These can be twofold and concern (a) the total number of elvers swimming and (b) their vertical movements.

a) Our data show that the total day-time catches are smaller than the night catches. By day we caught on an average 30 elvers a tide, but by night 116, i.e., 4 times as many. Hence we may conclude either that at sea elvers prefer to swim at night or that if they swim by day, they keep very close to the bottom, where they cannot be caught.
b) The vertical movements may be studied by comparing the catches of the bottom and surface nets. To facilitate this, surface catches have been expressed in percentages of the total catch per tide, without regard to the inequality between surface and bottom flow (Table 14). It is true that the surface percentages are weighted by this procedure relative to the bottom percentages, but as we compare surface percentages with each other only, our conclusions are not affected.

Table 14. The average catch of elvers (numbers) at the surface expressed as a percentage of the surface and bottom catches in the Wadden Zee.

The bracketed figures are the numbers of observations from which the average percentages have been derived.

	Night	Night to Day	Day	Day to Night
Flood	88 (22)	71 (7)	36 (12)	60 (6)
Ebb	74 (20)	48 (4)	7 (15)	0 (1)

The figures show that by night the majority of the elvers tend to stay near the surface, while by day they keep to the bottom. However, the vertical movement caused by the day-night rhythm is difficult to separate completely from tidal effects, for which reason both influences will be discussed together.

Comparing the catches at different stages of the tide we find that by night there is not much difference in the conduct of the elvers on the flood and ebb tides. It is true that the average percentage catches at the surface on the flood tide are somewhat higher than on the ebb, but they are both of much the same order of magnitude. This is not so for the day-time catches; by day, 36 % of the elvers at the surface were caught on the flood, while the corresponding number for the ebb is only 7 %. This difference may be explained in the following way. According to Mr. H. Postma (see also Canter Cremers, 1921) the turbulence in the water is on an average much greater on the flood than on the ebb tide. Hence bottom deposits are spread much more extensively through the water layers on the flood than on the ebb, and the water at the surface is rendered more turbid. Accordingly more elvers are attracted to the surface than when the water is relatively clear. Moreover, we must also reckon on the elvers being carried upwards more actively, and then staying there by their own powers of swimming. It is thus understandable that relatively more elvers are caught at the surface on the flood than on the ebb tide.

This conclusion, based upon the activity-light relation, is also supported in other ways by our observations. For instance, the surface catches made during twilight are intermediate between the respective day and night catches. Again, it will be noticed that the average catches in Table 14 reflect a gradually changing degree of light intensity in the water; the greatest contrast is shown by flood tide by night and ebb by day, while the remaining values lie between them. The difference between these two averages is statistically significant. Hence our observations indicate that on the average elvers swim at a relatively higher level on the flood tide than on the ebb, and that the most likely cause of this is the changing intensity of light in the water.

The phenomena discussed so far are mainly the indirect results of tidal movements. We may also consider the question of direct effect; for instance, do more elvers tend to be transported by the flood stream than by the ebb, as several authors suppose? Our observations are not well suited to a discussion of this matter, for we do not know exactly the number of elvers present at the time our observations were made. If on a particular ebb tide no elvers are present, it follows that our nets cannot catch any. Similarly if many are present on a particular flood many elvers will be caught, but it does not follow that elvers are transported by the flood and not by the ebb.

To investigate this matter, we must examine a series of observations made on subsequent days (so that we may suppose we fished the same stock of elvers) as, for instance, those of 20.—24. March 1950. The observations made in full daylight are omitted, for many elvers were probably not recorded then. There thus remain observations made during the night and at sunset and sunrise. The total quantities caught are 2697 elvers in 1900 minutes (142 elvers per 100 minutes) on the flood tide by twilight, and 2391 elvers in 2090 minutes (114 elvers per 100 minutes) on the ebb by night.

To interpret these figures we require to know the ratio of the flows at the different states of the tide. According to Mr. H. P o s t m a both tides transport practically the same amount of water. Because the average duration of the flood in the Wierbalg—where the observations were made—is less than the duration of the ebb, the flood stream must be stronger than the ebb stream.

Over 8 flood tides we were able to fish for 1900 minutes with both nets, so an average "fishable" flood tide at that time lasted 119 minutes. In the same way we see that an average "fishable" ebb tide lasted 249 minutes, that is, 2·1 times longer than the flood. This implies that the average flood flow must have been 2·1 times stronger than the average ebb flow during our observations. Assuming that our nets filtered the same amount of water we thus get the following relation:—

$$\text{flood transport} : \text{ebb transport} = \frac{142}{2 \cdot 1} : 114 = 1 : 1 \cdot 7.$$

It may be recalled that the flood tide observations were made at twilight and it is probable that for this reason some elvers were not

"catchable", despite the greater turbidity of the water, and the relation is probably weighted in favour of the ebb tide. Hence it appears that there is no reason to suppose that elvers choose the flood tide on which to be transported to their destination; it is more likely that rather the same number of elvers are swimming about on both flood and ebb tide. This is additional support for our view that tides exert practically no internal influence—if any—upon the behaviour of elvers.

The migration of the elver.

Our investigations suggested that the path followed by migrating elvers might be divided into two parts, that in the sea, and that near freshwater outlets. Although something of the characteristic behaviour of elvers near freshwater outlets has been discovered, we still know little about the orientation of elvers in such surroundings, so we shall not deal with it at present.

With regard to orientation and migration at sea, although we are better informed now, this subject requires more thorough discussion before it can be fully grasped. I believe I have formulated an explanatory hypothesis, which leads to a better understanding of the distribution of elvers, and which is in agreement with the numerous observations made.

Let us consider first the elver migration in the English Channel and North Sea. According to Schmidt (1906) elvers generally reach Brittany and Lands End in southern England in February. We know also that on an average elvers arrive at the Afsluitdijk in the last half of March. This indicates that a distance of some 900 km. is covered in about 45 days, giving an average daily speed of about 20 km. in the most favourable situation. At this speed elvers should first reach Denmark in the middle of April, which agrees with Schmidt's 1906 findings.

What we want to know is, How do elvers manage to travel at this speed? It can be attained in three ways, namely, passive transport by the water flow, swimming, or a combination of both.

Let us first consider the flow. In the region considered the tidal streams are the important features of the water movement. The conditions which elvers can encounter are as follows:—

	a)	b)	c)
night	1 flood tide	1 ebb tide	exceptionally 1 flood and ebb tide
intermediate period (sunrise or sunset occurs during a tide)	2 ebb tides	2 flood tides	—
day	1 flood tide	1 ebb tide	1 ebb and flood tide

To interpret these conditions we must remember that on the flood tide elvers usually swim at a higher level than on the ebb. In the Wadden Zee this is caused by the greater turbidity during the flood tide, as a consequence of the increased turbulence stirring up the

bottom deposits. According to Mr. H. Postma this will also happen in the North Sea and English Channel, although the bottom deposits will probably not be brought right up to the surface. But near the bottom, the water will be more turbid during the flood than during the ebb.

For our calculations we need to know the average speeds of the flood and ebb streams between the mouth of the English Channel and Holland. These figures have been computed by van Heusden (1943) from the "Atlas der Gezeiten der deutschen Seewarte" (1926). He used the positions numbered 4, 5, 67, 86, 94, 101, 111, 113, 117, 161, 162, 182, 183, 186, 187, and 189 in this atlas, and these positions probably lie on the migration route of the elver. According to van Heusden the average surface flood flow is 28 m./min., while that of ebb is 29 m./min. Flood lasts 401 minutes and ebb 370 minutes. Hence we get an average transport of 11·2 km. for the flood, and 10·7 km. for the ebb.

Let us now consider cases a) and b) together.

By night elvers will swim usually in the upper water layers, where the respective flows will transport them favourably at the rate of 0·5 km. in 2 days. According to our observations (Table 14) only a few elvers swim at the surface during the flood and in the bottom layers during the ebb. In this case they will also gain by the differences in stream speed at surface and bottom, if they act in this way persistently. By night the bottom of the sea will be dark; so elvers will not therefore swim close to it, and will be carried along by the flow, as our observations show. Their extra gain per 2 days will thus be small.

In the intermediate period, at this season the bottom of the English Channel and southern North Sea may be expected to be dark (Russell, 1931). Hence we may assume that elvers swim a little off the bottom during the ebb, and perhaps at a somewhat higher level during the flood. Thus their gain will be very slight, say $2 \times 0{\cdot}5$ km./2 days.

By day. We do not know whether elvers swim by day, but let us suppose that they do. On the ebb tide elvers will swim close to the bottom; in the most favourable case they will not be transported backwards. On the flood they swim higher in the water and are transported forward, let us say, the maximum distance of 11·2 km. Their maximal gain is then 11·2 km./2 days. We thus get a total of $0{\cdot}5 + 2 \times 0{\cdot}5 + 11{\cdot}2$ km./2 days $= 6{\cdot}4$ km./day. This may be slightly more, if the elvers behave by night in the manner described above.

Case c) is exceptional, but may be considered here for the sake of completeness.

By night. Reckoning as above, we get a gain of 0·5 km./day, perhaps somewhat more.

By day. For part of the day during the ebb tide the bottom is dark (Russell, 1931), and the elvers accordingly swim at a distance from the bottom and are carried some 3—4 km. backward. Maximal gain on the flood is 11·2 km., giving a total day-time gain of 7·7 km. The total

daily gain is at most 8·2 km., which agrees well with the value we found for cases a) and b).

A tidal transport of about 6·5 km./day, or somewhat more, we can understand, but this falls far short of the 20 km./day needed. Hence we are forced to assume that elvers cover a certain distance by active swimming, and they must do this both by day and by night. According to observations made by ter Pelkwijk (1938) and myself, the average speed at which elvers swim about is 15 cm./sec. or 13 km./day. This value added to that of 6·5, which we found, gives a transport of about 19·5 km./day, which fits very well with our earlier estimate, derived from the dates of arrival on various European coasts.

It must be remarked, however, that to reach the daily "mileage" the elvers need to swim in one direction, which is in the same line as the tidal streams. This might imply that elvers are able to recognize ebb and flood; on the ebb they swim against the stream, and on the flood they swim with it. One might expect them to be able to make this distinction when they are on the bottom, but how do they manage to keep their direction in the upper water layers, where they apparently lack any means of orientation? Deelder (1949a), however, proved the existence of an innate "sense of direction" in silver eels migrating to their spawning places. If silver eels possess such a sense, it is reasonable to assume that elvers also possess this sense. If this is so, elvers, whether swimming near the bottom or the surface, are able to follow a chosen direction. It is possible that the difference in turbulence enables elvers to distinguish between ebb and flood flows when they are on the bottom (although we obtained no support for this idea in the preceding section) and that they are able to "recollect" these directions when in the upper water layers.

Another possibility is that elvers keep to a direction with the help of the electric currents generated by the movements of sea water. The horizontal component of the current is perpendicular to the flow of the sea water. If elvers are able to perceive very small currents, they can align themselves with the water flow by taking up a position in which no electrical current runs from snout to tail or the reverse. Dr. P. Groen has estimated that in elvers this current would be almost 1×10^{-10} amp./mm^2. for a water speed of 1 m./sec., provided that the electrical resistance of elvers is the same as that of sea water. We do not know what current elvers can perceive, but Uzuha (1934) found that a catfish could perceive a current of 1×10^{-7} amp., which is 1000 times greater than the value mentioned above.

What are the consequences of these orientation hypotheses? Firstly, elvers travel in the same line as the tidal streams where these are present. This explains the arrival of many elvers on the coasts of Ireland, of western and southern England, of France, Spain, etc. ("Atlas der Gezeiten", 1926). Secondly, elvers evidently reach the southern North Sea through the Straits of Dover and migrate northwards, as the flood stream is north-going. Elvers reach the North Sea by the route north of England too (see Schmidt, 1906) and will migrate southward with

the south-going flood stream, reaching the east coast of England sometimes in considerable numbers (P e n t e l o w, private communication).

There is, however, a third explanation of these phenomena, which, I believe is the more plausible. We may recall that it is a very common characteristic in migrating birds (see D e e l d e r, 1949b) that they migrate in a certain direction with the exercise of an innate sense of direction. When these birds (land or sea birds) reach a distinct boundary, e.g., a coastline, they exchange this innate orientation for a visual method, i.e., they fly along the coastline in the direction which deviates least from the chosen direction. If the coastline disappears the birds revert to their innate orientation and proceed in their original direction.

With regard to elvers, let us suppose with V e r w e y (1949) that they have an eastward sense of direction. Elvers swimming in this direction after metamorphosis will sooner or later reach a coastline. Now it has been proved (see also D i e s e l h o r s t 1938) that eels can hear. On an oceanic coast such as the Atlantic coast of Europe, there will be surf, the beat of which we may assume elvers can hear, the more so because water transmits sound much better than air. Just as a man can move along the shore with his eyes closed, orientating himself with his ears towards the breakers, so may elvers be able to do it. In this connexion W e s t e n b e r g (1952) states that certain Indonesian fish are able to swim parallel to a coast; they are even able to keep along a certain depth contour. W e s t e n b e r g explains this feature not as due to the surf, but to the ruffled water surface sending sound vibrations downward which are reflected from the bottom. This will set up resonance with an average wave-length of four times the depth, so that a particular resonance frequency will correspond to a certain depth.

In correspondence with what is known of birds, would it not be reasonable to assume that elvers, when in the vicinity of land, discard their innate sense of direction and travel along the coast in that direction which deviates least from their original one, orientating themselves acoustically? It is to be remarked that the elvers would then be travelling in the same line as the tidal streams, generally with the flood and against the ebb stream. In this case, however, the elvers need not be able to distinguish between these streams, which greatly simplifies the hypothesis and is also in agreement with the conclusions reached in the preceding section.

This hypothesis is based upon proven facts; it is the combination of them which must be proved. This is a very difficult task, however, perhaps impossible at present, for the technical facilities for making the necessary observations are not yet available.

Summary.

Investigations have been carried out on the factors influencing the migration of elvers at sea. These investigations have comprised the

collection and study of statistical data as well as the making of observations at sea. The main results are as follows:—

The intensity of the elver migration shows some decline in the period studied, namely, 1936—1950; the decline cannot be explained.

The minimum value of the range of sea water temperature in which elvers migrate is about 4·5°C. Temperature and intensity of migration are not correlated.

A relation exists between light intensity and elver activity, but there is no correlation between moon phase and migration intensity.

The rate of water discharge and the consequent fall in salinity some distance away from freshwater outlets do not affect the migration of elvers in the sea.

Spring and neap tides have no differential effect on elver migration, nor can a direct effect be traced directly to the direction of the tidal streams. Apparent connexions between tidal streams and elver migration near freshwater outlets must be ascribed to local factors.

It appears that elvers travel both by day and by night at sea; at night they swim at a much higher level in the water than by day, which must be ascribed to the differences in light intensity. As turbidity is higher with the flood than with the ebb in our waters, elvers travel at a higher level on the flood than on the ebb. Consequently over a large part of their migration, transport is effected by the tidal streams.

A hypothetical explanation of the migration of the elvers at sea is offered.

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CONTRIBUTION
A L'ETUDE DU MERLU DE L'ATLANTIQUE.

Préface.

Le "Problème du Merlu".

Des textes anciens montrent que, depuis les temps historiques, la pêche du merlu (*Merluccius merluccius* Linné) a toujours été une importante ressource pour l'économie de la pêche dans les pays de l'Europe occidentale; particulièrement en France, en Espagne et au Portugal où, au large des côtes, dans des eaux relativement chaudes et salées, n'apparaît pas la morue (*Gadus callarias* Linné), autre Gadidé des mers continentales, froides et peu salées, ressource majeure de l'industrie des pêches dans les pays d'Europe septentrionale.

Le merlu se pêchait autrefois à la ligne, parfois au filet. Le développement rapide et intense de la pêche aux arts traînants depuis le début du siècle présent, le perfectionnement du chalut, l'augmentation progressive de son pouvoir de capture, l'écoulement facile de ce poisson sur les marchés, firent qu'on le rechercha de plus en plus.

L'exploitation exagérée des lieux de pêche *limités* du merlu se traduisit, dès 1910, par une diminution sensible des apports des chalutiers opérant aux accores du Plateau Continental Atlantique, habitat normal de ce poisson qui ne s'en écarte qu'à l'époque de la reproduction, au printemps ou en été, pour y revenir la fraie terminée.

Les chalutiers furent ainsi entraînés à aller le rechercher vers le sud; à la bordure du Plateau Continental, dans le Golfe de Gascogne, sur les côtes d'Espagne, du Portugal, puis, sur celles du Maroc.

Ces nouveaux fonds de pêche, exploités intensivement, comme les précédents, s'épuisèrent progressivement à leur tour. Il fallut aller encore plus loin. Les chalutiers prospectèrent alors la Pente Atlantique, au large des côtes de Mauritanie et du Sénégal; cependant que, la pêche continuant toujours aux accores du Plateau Continental Européen avec

des moyens sans cesse accrus, il est devenu flagrant que son avenir risque fort d'être irrémédiablement compromis si elle n'est pas limitée dans un bref délai.

Les apports des chalutiers opérant au large des côtes d'Afrique devenant de plus en plus réguliers, il apparut bientôt aux biologistes, penchés sur le "Problème du Merlu", que les merlus capturés aux accores du Plateau Continental Africain se montraient différents par certains caractères morphologiques de l'espèce européenne: (*Merluccius merluccius* Linné) et qu'ils pouvaient constituer des variétés, sinon des espèces distinctes de ce merlu européen.

Le "Problème du Merlu" se présentait désormais avec un double intérêt: économique et scientifique.

C'est ce qui a conduit le Comité Atlantique du Conseil International pour l'Exploration de la Mer à entreprendre, avec la collaboration des laboratoires maritimes, une étude coordonnée de la systématique du genre *Merluccius* Rafinesque, de la biologie et de la pêche des différentes espèces du genre dans l'Atlantique Nord-Est.

Le programme de ces recherches a été établi au cours d'une réunion spéciale du Comité Atlantique, dite "Colloque du Merlu", qui s'est tenue à Amsterdam, le Mardi 3 Octobre 1951, avec l'ordre du jour suivant:—

Ordre du Jour.

I. Caractères génériques — Genre *Merluccius* Rafinesque.
II. Caractères spécifiques — *Merluccius merluccius* L.
III. Espèces voisines de *Merluccius merluccius* L.
Espèces ou variétés de merlus dans l'Atlantique.
IV. Distribution géographique et bathymétrique.
V. Etude biométrique
a) Caractères métriques.
b) Caractères numériques.
c) Caractères physiologiques.
d) Fiche ichthyométrique des différentes espèces,
Variétés ou populations géographiques de merlus.
e) Interprétation des résultats.
VI. Croissance du merlu.
a) en Atlantique.
b) en Méditerranée.
VII. Déplacements du merlu.
Expériences de marquage.
VIII. Constitution du stock. Mensurations.

Les rapports suivants ont été présentés à ce Colloque et leur publication dans le *Journal du Conseil* recommandée par le Comité Atlantique, le Comité Consultatif, et, enfin, le Bureau du Conseil International pour l'Exploration de la Mer.

J. le Gall.

A. Les Espèces et Variétés du Genre *Merluccius* Rafinesque.

Par

Jean le Gall.

Depuis que G i l l (1884), se basant essentiellement sur les caractères ostéologiques, a séparé les vrais merlus des autres Gadidae et des Macruridae en créant pour eux la famille des Merlucciidae, reconnaissable, d'autre part, à l'absence totale de barbillon à la mandibule, N o r m a n (1937), revisant la taxonomie du genre *Merluccius* Rafinesque[1]) a distingué sept espèces différentes de merlus, toutes très voisines, dont les caractères distinctifs ont été précisés dans un travail plus récent de T. J o h n H a r t (1948).

Quatre caractères d'inégale valeur, dont plusieurs restent discutables, ont été retenus par T. J o h n H a r t dans cette distinction. Ce sont:—

— La grandeur relative des écailles, déterminée par leur nombre en série longitudinale immédiatement au-dessous de la ligne latérale;
— Le nombre de branchiospines sur la branche inférieure de l'arc branchial antérieur;
— L'extension de la pectorale n'atteignant pas ou s'étendant au delà de la nageoire anale;
— La relation entre la hauteur du corps (H) et la longueur totale (L).

Néanmoins, tout en montrant la nécessité de recherches ultérieures, T. J o h n H a r t a distingué ainsi les sept espèces du genre *Merluccius*.

A. Moins de 115 écailles en ligne longitudinale.

Pectorales { atteignant ou dépassant l'origine de l'anale. *M. gayi* (Guichenot)
n'atteignant pas l'origine de l'anale. *M. bilinearis* (Mitchill)

B. De 130 à 150 écailles en ligne longitudinale.

Branchiospines sur la branche inférieure du 1er arc branchial
— Voisin de dix ou moins ..... *M. merluccius* (Linneus)
— Nettement supérieur à dix .....
— Plus de dix .....

Pectorales { n'atteignant pas l'origine de l'anale: *M. hubbsi* Marini
atteignant ou dépassant l'origine de l'anale:
$\frac{\text{Longueur du corps}}{\text{Hauteur du corps}}$: (égale ou supérieure à 7): *M. productus* (Ayres)
(nettement inférieure à 7): *M. capensis* Castelnau

[1]) Le nom générique de *Merluccius* adopté par N o r m a n (1937) a été retenu dans ce texte à la place de *Merlucius* encore souvent cité par les Auteurs.

C. Plus de 150 écailles en série longitudinale: *M. australis* (Hutton) (d'après T. J. Hart.)

Parmi ces sept espèces, trois existent dans le Pacifique:—

Hémisphère Nord: *M. productus* (Ayres) (Côte Amérique du Nord)

Hémisphère Sud { *M. gayi* (Guichenot) (Côte Amérique du Sud)
M. australis (Hutton) (Nouvelle Zélande)

et quatre dans l'Atlantique:—

Hémisphère Nord { *M. merluccius* (Linneus) (Côtes Europe et Afrique du Nord)
M. bilinearis (Mitchill) (Côte Amérique du Nord)

Hémisphère Sud { *M. capensis* Castelnau (Afrique du Sud)
M. hubbsi Marini (Côte Est Patagonie)

De ces quatre espèces atlantiques, deux sont particulières à la côte est: l'une, dans l'hémisphère nord, *Merluccius merluccius* (Linneus), dont la limite d'extension méridionale peut être fixée dans le voisinage du Tropique du Cancer, l'autre, dans l'hémisphère sud, *Merluccius capensis* Castelnau, dont la limite septentrionale normale ne dépasserait guère le Tropique du Capricorne.

Cependant, les observations récentes ont montré que, dans la zone équatoriale, entre les deux tropiques, existerait une huitième espèce, déjà envisagée comme race ou variété de l'espèce Nord-atlantique *M. merluccius* par G. Belloc (1929), puis admise plus récemment par J. Cadenat comme espèce distincte: *M. senegalensis*, qui occuperait, dans l'Atlantique Nord, l'espace laissé vacant entre les aires de distribution de *M. merluccius* au nord et *M. capensis* au sud.

Allant plus loin, J. Cadenat ferait également une autre espèce distincte avec les merlus capturés dans la zone équatoriale, au sud de l'Equateur, sur le plateau continental, au large du Congo.

La discontinuité de la distribution du genre Merlu dans l'Atlantique oriental; les limites imprécises de l'aire d'extension de *M. merluccius* d'une part, et de *M. capensis* d'autre part, la variation possible des caractères morphologiques de ces deux espèces à la limite de leur domaine; l'existence possible des deux nouvelles espèces équatoriales, et enfin, l'importance économique du genre justifient l'intérêt apporté par le Comité Atlantique du Conseil International pour l'Exploration de la Mer aux problèmes soulevés par les résultats des observations faites au cours de ces dernières années ainsi que la collaboration qui s'est établie au sein de ce Comité pour élaborer un plan de travail commun dont les grandes lignes ont été ainsi définies lors de la réunion du Comité le Mardi 3 Octobre 1951.

B. Note sur le Merlu de la Côte d'Afrique.

(Maroc et Rio de Oro).

Par

R. Letaconnoux.

G. Belloc (1937), en signalant sa présence au large des Iles du Cap Verd, a considéré le merlu dit de Mauritanie comme une race locale du merlu européen (*M. merluccius*), bien qu'il eût une moyenne vertébrale nettement différente et plus forte que celui-ci: 54·09, contre 50·48 à 51·15.

Revenant sur le même sujet et sans pouvoir conclure faute d'échantillons en nombre suffisant, J. T. Hart (1946—1948) a laissé la question pendante.

Au cours de la campagne du navire océanographique "Président Théodore Tissier" en 1950, nous avons pu examiner un certain nombre de merlus capturés au chalut le long des côtes du Maroc et du Rio de Oro. Des observations faites, il apparaît que, depuis la région de Safi au Maroc, on rencontre, en descendant vers le sud, un merlu différent très nettement du merlu européen *M. merluccius* Linneus par sa moyenne vertébrale nettement supérieure (53·3 au lieu de 51) et par le nombre moyen de branchiospines présentes sur la branche inférieure du premier arc branchial (14·5 au lieu de 9·8), caractère permettant de distinguer immédiatement ce merlu de Mauritanie du merlu européen et de retenir la distinction déjà faite par G. Belloc, puis, par J. Cadenat, qui a proposé le nom de *Merluccius senegalensis* pour cette nouvelle espèce.

La présence du merlu de Mauritanie et du Sénégal ayant été constatée dans la région du Cap Cantin au cours de cette campagne, la limite septentrionale de l'aire de distribution de la nouvelle espèce *M. senegalensis* est à reporter dans la région du Cap Cantin où elle coexiste avec l'espèce européenne *M. merluccius*.

C. Les Merlus des Côtes Atlantiques du Maroc.

Par

Claude Maurin.

LE merlu est le poisson le plus pêché au Maroc. Sa pêche est pratiquée au chalut sur le plateau continental, de part et d'autre de la zône de Dendrophyllies qui, devant Casablanca, se situe par des fonds de 110—180 m. environ. On la pratique également sur le talus du plateau; mais rares sont les chalutiers qui s'aventurent si loin et la plus grande partie de la pêche est effectuée sur des fonds de 60 à 150 m.

Les engins utilisés sont principalement des chaluts de type espagnol ou italien qui, jusqu'en 1951, étaient constitués par des nappes de très petites mailles (10 à 15 mm.).

I. Taille des Merlus de la région de Casablanca par rapport à la profondeur

Pendant les années 1949 et 1950, 7740 merlus provenant de la région de Casablanca ont été mesurés. Tous ont été capturés avec des filets à petites mailles (10 à 15 mm.),

dont: 5102, pris par des fonds de 50 à 150 m., soit en deçà de la zône de coraux. Leur taille varie entre 10 et 70 cm.; 82 % d'entre eux n'atteignent pas 25 cm. et sont immatures.

— 2658, pris par des fonds supérieurs à 150 m., soit au delà des coraux. Leur taille varie entre 10 et 100 cm., 33 % seulement d'entre eux ont une taille inférieure à 25 cm. (Tableau No. 1).

Deux faits peuvent être retenus de ces observations. L'augmentation de la taille avec la profondeur est assez nette. Mais le nombre d'immatures est encore élevé par les grands fonds. Il semble que le merlu s'enfonce davantage vers les grandes profondeurs à mesure qu'on approche des régions tropicales.

De plus, en 1951, (voir graphique, Figure 1), une expérience faite par des fonds de 50 à 150 m. avec un chalut à mailles de 35 mm, montre que 38 % seulement d'entre eux (contre 82 % avec les mailles de 10—15 mm.) sont immatures.

Tableau 1. Taille des Merlus pêchés à Casablanca avec le Filet à Mailles de 10—15 mm.

Tailles en cm.	Profondeur de 50 à 150 m.		Profondeur supérieure à 150 m.	
	Fréquence	Pourcentage	Fréquence	Pourcentage
10 (5 à 14 cm.)	439	8·60	46	1·75
20 (15 à 24 cm.)	*3737*	*73·25*	782	29·64
30 (25 à 34 cm.)	895	17·55	*1469*	*55·69*
40 (35 à 44 cm.)	29	0·56	261	9·89
50 (45 à 54 cm.)	1	0·02	40	1·52
60 (55 à 64 cm.)	1	0·02	7	0·27
70 (65 à 74 cm.)	—	—	14	0·53
80 (75 à 84 cm.)	—	—	14	0·53
90 (85 à 94 cm.)	—	—	4	0·15
100 (95 à 104 cm.)	—	—	1	0·03
Nombre total	5102		2638	

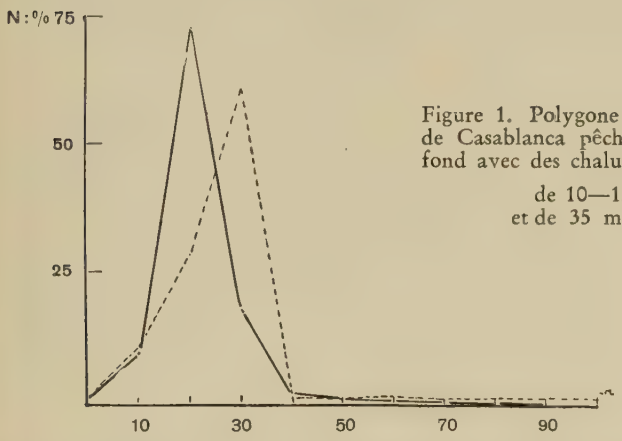

Figure 1. Polygone de variation des merlus de Casablanca pêchés par 50 à 150 m. de fond avec des chaluts à mailles de 10—15 mm. ——— et de 35 mm. - - - - -

II. Morphologie du Merlu de la région nord du Maroc (Casablanca—Rabat). (Observations faites de 1949 à 1951)

A. Proportions du corps.

Les indices suivants ont été calculés par rapport à la longueur totale mesurée du bout du museau à l'extrémité de la nageoire caudale; longueur latérale de la tête: $\frac{100\ T}{LT}$; distance prédorsale: $\frac{100\ D}{LT}$; distance préanale: $\frac{100\ A}{LT}$.

Pour des lots de 306, 358, et 223 jeunes merlus de petite taille (9 à 35 cm.) et pour des lots moins homogènes de 35 et 21 adultes (45 à 100 cm.) la comparaison des résultats montre que:—

a) $\frac{100\ T}{LT}$ varie entre 25 et 31 pour les jeunes, (mode 27/28) et pour les adultes entre 23 et 29 (mode 26/27). Ceci indique que la longueur relative de la tête décroît avec la taille, donc avec l'âge.

b) $\frac{100\ D}{LT}$ varie de 26 à 31 pour les jeunes (mode 28/29) et pour les adultes de 23 à 30 (mode 27/28): la distance prédorsale décroît avec la taille.

c) $\frac{100\ A}{LT}$ varie de 35 à 44 chez les jeunes (mode 39) et pour les adultes de 41 à 46 (mode 42). Dans ce cas la valeur de l'indice croît avec la taille.

B. Caractères méristiques.

Les rayons des première et deuxième dorsales, les vertèbres et les branchiospines des 1ers arcs branchiaux droit et gauche ont été dénombrés (Tableau No. 2).

Les résultats obtenus en 1949 et 1950 étaient très voisins. En 1951, quelques différences avec les merlus des années précédentes se présentèrent ainsi:—

Année	Nombre moyen de rayons de la 1ère dorsale	Nombre moyen de rayons de la 2ème dorsale	Nombre moyen de vertèbres
1949	9·96	38·06	50·58
1950	9·94	38·07	50·57
1951	9·86	38·22	50·82

Tableau 2. Merlu de Casablanca.

Variation du nombre de rayons de la 1ère dorsale

	Nombre de rayons 9	10	11	Total	Nombre moyen	σ ±	Flm ±
1949	22	193	8	223	9·94	±0·36	±0·08
1950	25	320	13	358	9·967	±0·325	±0·05
1951	60	231	15	306	9·86	±0·47	±0·09

Variation du nombre de rayons de la 2ème dorsale.

	Nombre de rayons 35	36	37	38	39	40	41	Total	Nombre moyen	σ ±	Flm ±
1949	3	10	53	76	65	16	—	223	38·06	±1·06	±0·23
1950	1	5	93	142	104	13	—	358	38·07	±0·88	±0·155
1951	—	10	53	121	100	20	1	305	38·22	±0·93	±0·17

Variation du nombre de vertèbres.

	Nombre de vertèbres 49	50	51	52	53	54	55	Total	Nombre moyen	σ ±	Flm ±
1949	13	105	116	21	1	—	—	256	50·58	±0·72	±0·152
1950	7	151	190	9	—	—	—	358	50·57	±0·715	±0·124
1951	1	97	157	38	1	—	1	295	50·82	±0·712	±0·138

Variation du nombre de branchiospines.

	Nombre de branchiospines des 1ers arcs branchiaux droit et gauche 9	10	11	12	13	14	Total des individus
1950	5	114	7	—	2	2	65
1951	100	704	50	—	—	2	428

Il serait sans doute prématuré de tirer des conclusions de ces variations, mais il est tout de même intéressant de noter que de telles variations sont corrélatives d'une nette diminution de la température hivernale (1·5° à 2°C.) par rapport aux deux hivers précédents et qu'elles pourraient traduire un certain glissement vers le sud, des merlus de la plate-forme ibéro-marocaine.

Le dénombrement des branchiospines, dont M. Letaconnoux nous avait signalé tout l'intérêt, a été entrepris en 1950 et continué en 1951. Cette étude nous a permis de distinguer deux formes de merlus cohabitant sur les côtes du Maroc.

1° le merlu type, *Merluccius merluccius* L. dont la moyenne vertébrale est de 50·6 à 50·8 environ dans notre région et qui possède de 9 à 10 branchiospines.

2° le merlu dit "merlu noir" dont M. Cadenat a fait récemment une espèce, *Merluccius senegalensis*.

Le dernier, rare dans la région de Casablanca, se rencontre dans le sud avec l'espèce septentrionale. Nous étudierons plus loin ses caractéristiques.

C. Contenu stomacal.

Un premier inventaire du contenu stomacal de 290 merlus pêchés dans la région de Casablanca de Janvier à Mars 1951 a donné les résultats suivants:—

37·6 % des estomacs étaient vides,
21·7 % contenaient des débris indéterminables,
24·5 % des anchois (*Engraulis encrasicholus* L.),
13·8 % des crustacés, en particulier des crevettes
Parapenaeus longirostris Lucas;
Plesionika heterocarpus Costa;
Plesionika sp.; *Chlorotocus gracilipes* Milne Edwards
et des Euphausiacés,
1·4 % des Céphalopodes (*Loligo sp. Sepiola sp.*),
1·0 % des poissons divers (1 sardine, 1 merlu, 1 poisson plat).

D. Tératologie.

Nous avons observé deux merlus (*Merluccius merluccius* L.) présentant certaines anomalies.

L'un d'eux, pêché dans la région de Casablanca le 18 Avril 1951 a le lobe caudal extrêmement court, la nageoire caudale débutant immédiatement après le dernier rayon de la deuxième dorsale; l'indice $\frac{100\ T}{LT}$ a la valeur de 33·6 au lieu de 27 à 28 chez les individus normaux de la même taille.

Le second, pêché dans le secteur de Rabat le 19 Janvier 1951 par 100 m. de fond présente une déformation de la tête: à la hauteur des yeux, le front s'infléchit brusquement pour rejoindre la machoire supérieure qui est nettement plus courte que la mandibule. L'arrière de la tête et le reste du corps sont normaux.

III. Les Merlus du sud (Agadir—Oued Draa—Rio de Oro et Mauritanie).

Les merlus provenant du sud marocain, du Rio de Oro et de la Mauritanie présentent, pour les caractères étudiés, des fréquences et valeurs moyennes nettement différentes de celles des merlus de Casablanca.

Les lots examinés sont les suivants:—

— 14 merlus pêchés en 1950 à Agadir (taille 20 à 24 cm.)
— 40 merlus pêchés en 1950 au Cap Juby (taille de 20 à 40 cm.)
— 39 merlus pêchés en 1950 au Cap Blanc de Mauritanie (taille de 35 à 65 cm.)
— 20 merlus pêchés en 1951 entre l'Oued Noun et l'Oued Draa (taille de 17 à 29 cm.).

Tableau 3.

Variation du nombre de rayons de la 1ère dorsale.

	Nombre de rayons				Nombre moyen de rayons	Nombre total d'individus
	9	10	11	12		
Casablanca	107	744	36	—	9·92	887
Agadir	1	4	9	—	10·57	14
Oued Draa	4	9	7	—	10·21	20
Cap Juby	4	21	15	—	10·27	40
Mauritanie	—	15	20	4	10·71	39

Variation du nombre de rayons de la 2ème dorsale.

	Nombre de rayons								Nombre moyen de rayons	Nombre total d'individus
	35	36	37	38	39	40	41	42		
Casablanca	4	25	199	339	269	49	1	—	38·12	886
Agadir	—	—	—	—	6	5	3	—	39·78	14
Oued Draa	—	—	—	5	5	5	5	—	39·50	20
Cap Juby	—	2	3	9	8	8	10	—	39·17	40
Mauritanie	—	—	—	3	11	15	7	3	39·89	39

Ces différences apparaissent dans le Tableau No. 3. Le dénombrement des vertèbres et des branchiospines (arc droit et arc gauche), en particulier, permet de séparer nettement le merlu méridional (*Merluccius senegalensis* de Cadenat) qui, selon nos propres observations, possède de 52 à 55 vertèbres (mode 53) et de 13 à 16 branchiospines (mode 14/15).

Pour les rayons de nageoires dorsales, les différences entre les deux espèces sont moins marquées: le merlu méridional possède de 10 à 12 rayons à la 1ère nageoire (mode 10). Chez le merlu septentrional (*Merluccius merluccius* L.) il y a de 9 à 11 rayons (mode 9).

La 2ème nageoire dorsale présente de 37 à 42 rayons (mode 40) chez le merlu méridional contre 35 à 41 (mode 38) chez le merlu septentrional.

En ce qui concerne la coloration externe, la différence entre les deux espèces est plus délicate à établir. Les muqueuses sont nettement plus foncées chez l'espèce méridionale.

Le pourcentage de merlus type septentrional (*M. merluccius* L.) est plus élevé dans le lot du Cap Juby que dans les autres lot. Le trop petit nombre d'individus étudiés ne nous permet pas de tirer de conclusions plus complètes. Notons seulement que les profondeurs auxquelles ces spécimens ont été pêchés sont environ:—

50 m. à Agadir; 40—50 m. à l'Oued Draa; 125 m. au Cap Juby; 80 m. en Mauritanie.

Tableau 3, Suite.

Variation du nombre de vertèbres.

	Nombre de vertèbres							Nombre moyen de vertèbres	Nombre total d'individus
	49	50	51	52	53	54	55		
Casablanca	21	353	463	68	2	—	1	50·65	908
Agadir	—	—	2	1	6	4	1	53·07	14
Oued Draa	—	1	7	1	9	1	1	52·25	20
Cap Juby	—	6	12	7	10	4	1	51·95	40
Mauritanie	—	1	2	13	19	4	1	52·69	39

Variation du nombre de branchiospines.

	Nombre de branchiospines des 1ers arcs branchiaux droit et gauche								Nombre total d'individus
	9	10	11	12	13	14	15	16	
Casablanca	105	818	57	—	2	4	—	—	493
Agadir	1	3	—	—	6	10	8	—	14
Oued Draa	2	12	2	—	—	16	8	—	20
Cap Juby	4	31	5	—	6	13	18	3	40
Cap Blanc	—	—	—	—	—	4	8	—	12

En résumé, des quelques observations qui précèdent il se dégage que:—

1°) les merlus du secteur nord marocain (Casablanca) constituent un groupe relativement homogène.

2°) au contraire, au sud du Maroc, au Rio de Oro et en Mauritanie, 2 formes cohabitent: le merlu septentrional et le merlu méridional, forme mélanique, dont nous essayerons ultérieurement de déterminer les domaines respectifs.

D. Note au Sujet des Merlus de la Région de Dakar.

Par

J. Cadenat.

LE matériel examiné les 24 Avril, 1er et 14 Juin 1951 provient des campagnes de pêche effectuées par le chalutier "Gérard Tréca" sur les fonds de 120 à 150 mètres au sud-ouest de la presqu'île du Cap Vert.

Les observations faites, portant sur plus de 50 individus permettent de me confirmer dans l'opinion qu'il s'agit d'une espèce différente du *Merluccius merluccius* typique des côtes d'Europe, que j'ai désignée sous le nom de *M. senegalensis*.

Toutefois l'examen de ce matériel faisant apparaître certaines variations, le tableau comparatif, ainsi que la clef dichotomique que je

Tableau comparatif

des caractéristiques les plus importantes de quelques poissons appartenant au genre *Merluccius*.

Provenance des échantillons examinés	Région de Cape Town	Au large de l'embouchure du Congo	Parages de la presqu'île du Cap Vert	Méditerranée au large de Castiglione
Nombre d'exemplaires examinés	1	2	61	2
Standard length (l) en mm.	545	236 et 325	130 à 326	165 et 177
Dorsale	X/40[1])	X/38 et X/39	XI/38 à XI/40	IX/38 et X/39
Anale	39	36 et 37	36 à 39	36 et 37
Nombre de branchiospines sur le premier arc[2])	6+13	2+8 et 2+8	2+7 — 4+12[5])	2+8 et 2+8
Nombre de vertèbres[3])	51	53	53 à 56	52
Longueur des Pectorales (P) en % l	18·8	20·9 et 21·0	18·8 à 20·1	15·0 et 15·1
Longueur de P en % de celles de la tête	62·2	65·1 et 68·5	66 à 75	51·0 et 53·4
Longueur des Ventrales en % de celle des P	ca. 70	ca. 70	68 à 80 %	ca. 100
Ecailles en ligne longitudinale[4])	130—140	98 à 105	140 à 155[6])	ca. 150

[1]) Les *M. capensis* ont généralement XI épines à la première dorsale, chez l'exemplaire examiné il semble que la dernière ait été atrophiée.

proposais pour différencier les diverses espèces de merlus de l'Atlantique oriental et de la Méditerranée, doivent subir quelques légères modifications.

Clef dichotomique

des principales espèces de merlus de l'Atlantique oriental et de la Méditerranée.

A/ Première dorsale à X épines.
10 ou 11 branchiospines bien développées sur le premier arc branchial: dont 8 ou 9 sur le bord inférieur (du moins chez les individus dépassant 20 cm. de longueur totale).

B/ Ecailles petites et nombreuses (on en compte au minimum 135 et jusqu'à 160 sur une ligne longitudinale).

C/ Pectorales nettement plus longues que les ventrales; leur longueur est égale à environ les $^2/_3$ de celle de la tête; (moyenne vertébrale environ 51) ..... *M. merluccius atlanticus*

CC/ Pectorales de même longueur que les ventrales; cette longueur égale environ la moitié de celle de la tête (moyenne vertébrale environ 52) ..... *M. merluccius mediterraneus*

BB/ Ecailles nettement plus grandes (environ 100 sur une ligne longitudinale (moyenne vertébrale environ 53) ..... *M. polli*[1])

AA/ Première dorsale à XI épines; au moins 14 branchiospines bien développées sur le premier arc branchial, dont 11 à 14 sur le bord inférieur (du moins chez les individus dépassant 20 cm. de longueur totale).

D/ Branchiospines au nombre de 6+13 à 14 (moyenne vertébrale environ 51) ..... *M. capensis*

DD/ Branchiospines au nombre de 3 ou 4+11 ou 12 (moyenne vertébrale environ 54 à 55) ..... *M. senegalensis*

[1]) Dédiée au Dr. P o l l de Tervuren (Belgique) qui a capturé cette espèce au cours de la croisière du Chalutier "Nordende II" en 1948.

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[2]) Les exemplaires de *M. merluccius* des côtes d'Europe ont généralement $^2/_8$ branchiospines sur le premier arc branchial.

[3]) La moyenne vertébrale des *Merluccius* de l'Atlantique varie de plus de 51 au nord (Irlande) à moins de 50·5 au sud (Mauritanie).

[4]) Chez *M. merluccius* de l'Atlantique ce chiffre varie de 140 à 160.

[5]) Il semble bien que le nombre des branchiospines développées soit assez variable chez les jeunes individus (dont la longueur totale est égale ou inférieure à 20 centimètres).

Tous les individus examinés à ce point de vue ont un nombre de *branchiospines développées* variant de 2+7 à 8+10 pour des tailles comprises entre 14 et 19 centimètres de longueur totale; à partir de cette taille et jusqu'aux plus grands examinés (36 cm.) ces nombres ont constamment été de 3 ou 4+11 ou 12.

Il est à noter que si l'on tient compte qu'il existe en avant des *branchiospines développées*, des plages pouvant être considérées comme des *bases de branchiospines* non développées, on constate que les sommes sont alors, dans tous les cas, de 3 ou 4+14 à 16.

[6]) Il est assez difficile d'obtenir des individus de cette espèce chez lesquels le compte des écailles puisse être fait d'une manière indiscutable; les chiffres donnés sont des chiffres approximatifs et ont été comptés sur les individus les moins détériorés par les moyens de pêche et de transport.

Merluccius senegalensis

Variation avec la taille du nombre des branchiospines sur le premier arc branchial.[1])

Longueur totale en mm.	Détail des branchiospines	Total
143	1+2+ 7+VIII	3+15=18
145	3+ 8+VII	3+15=18
148	3+ 8+VI	3+14=17
152	1+2+ 9+VI	3+15=18
157	3+ 8+VI	3+14=17
157	3+ 9+VI	3+15=18
160	3+ 9+?	3+
163	1+3+ 9+VI	4+15=19
168	3+ 9+?	3+
172	1+3+ 9+V	4+14=18
195	4+11+?	4+
206	4+11+?	4+
229	3+12+V	3+17=20
230	4+11+V	4+16=20
235	4+12+IV	4+16=20
285	1+3+12+?	4+
290	1+3+12+IV	4+16=20
296	4+11+V	4+16=20
302	4+12+III	4+15=19
312	1+3+11+IV	4+15=19
314	4+12+IV	4+16=20
323	3+12+IV	3+16=19
325	4+12+IV	4+16=20
330	1+3+12+IV	4+16=20
352	1+3+11+IV	4+15=19
357	4+12+III	4+15=19
360	4+12+IV	4+16=20

[1]) Dans la colonne Détail des branchiospines
— en chiffres romains: plages nues ou bases de branchiospines non développées.
— en chiffres arabes: branchiospines bien développées; les premiers chiffres s'appliquent à la partie supérieure, les autres à la partie inférieure de l'arc.

Moyenne vertébrale.

	Nombre d'individus examinés ayant le nombre suivant de vertèbres[1]) 53	54	55	56	Moyenne vertébrale
Exemplaires pêchés par le "Président Théodore Tissier" fond des Mamelles Mai 1936					54·09
18 Juin 1949	1	1	—	—	53·5
24 Avril 1951	—	3	—	—	54
6 Juin 1951	—	5	5	1	54·63
15 Juin 1951	—	1	4	3	55·25
Pour les 24 exemplaires de 1949 et 1951	1	10	9	4	54·66

[1]) Ces vertèbres se décomposent en:
— 6 cervicales.
— 19 à 21 abdominales ou thoraciques.
— 28 à 30 caudales (y compris l'urostyle).

Contenus Stomacaux.

La base de la nourriture des merlus du Sénégal aux divers lieux et époques de capture était constituée par des *Synagrops microlepis* Norman qui même, le plus souvent, représentaient la totalité du contenu stomacal. J'ai pu dénombrer jusqu'à 12 *Synagrops* de 7 à 9 cm. de longueur totale, dans l'estomac d'un seul merlu de moins de 25 cm. de longueur totale.

E. Note Préliminaire sur le Merlu des Mers Tunisiennes.

Par

H. Heldt.

I. Nom local. En Tunisie, le merlu, *Merluccius merluccius* L., est, comme en bien d'autres contrées méditerranéennes, dénommé merlan.

II. Répartition. Les chalutiers le trouvent dans les fonds vaseux et à des profondeurs relativement grandes 100 à 300 mètres et plus. Il ne se rencontre pas sur les fonds durs et il est moins abondant au voisinage de la côte.

Cet habitat conditionne sa répartition géographique: c'est principalement sur la côte nord de Tunisie (région au large de l'île Plane et de Zembra, Canal des Esquerquis) qu'il est pêché. Au large de la côte orientale, il se localise dans quelques fosses vaseuses, mais les apports des chalutiers de La Goulette (côte nord) sont trois fois plus importants que ceux de l'ensemble des ports de la côte est.

Merluccius merluccius ne se rencontre pas dans le Golfe de Gabès.

III. Production. La proportion de merlu dans les apports des chalutiers est d'environ 20 % du poisson pêché. Le poisson de chalut constituant par ailleurs le tiers de la production totale, le merlu apparaît comme une espèce importante sur les marchés tunisiens où plus de 600 tonnes sont vendues annuellement.

Taille. La taille moyenne des sujets est petite. Les plus beaux exemplaires ont ici la grandeur des "merluchons" débarqués dans les ports européens.

Croissance. L'abondance de sujets de petite taille justifie l'impression de nanisme de l'espèce en Méditerranée — on en a fait une race naine.

Une preuve de cette conception se trouverait peut-être dans le fait que des exemplaires de petite taille se trouvent avoir des glandes sexuelles à maturité et seraient ainsi des sujets adultes. Mais nous ne saurions déterminer leur âge par l'examen des écailles, car nous n'avons jamais trouvé, chez le merlu de Tunisie, d'écailles présentant des anneaux d'hiver nettement marqués.

Dans certains cas, par contre, les otolithes semblent "marquer". Nous en avons prélevé une collection dont l'étude sera faite par R. L e t a c o n n o u x.

Epoque de ponte. S'étage sur presque tous les mois de l'année. Nous avons trouvé des femelles "bouvardes" en Mars, et d'autres qui, fin Août, n'avaient pas terminé leur ponte.

Nombre de vertèbres. Le nombre des vertèbres varie de 51 à 53. La moyenne vertébrale, calculée sur 25 individus, a été trouvée égale à 51·92, chiffre très voisin de celui de L e t a c o n n o u x pour les merlus d'Atlantique (52·04).

Le nombre des vertèbres cervicales est remarquablement constant: 6.

Celui des vertèbres thoraciques est de 19 mais peut être seulement de 18 (8 % des cas).

Les vertèbres caudales sont au nombre de 26, 27, ou 28. (27 dans 68 % des cas).

Indices biométriques. Le tableau ci-dessous donne la valeur des indices:

$$T_i = \frac{100\ T}{L} \qquad D_i^1 \quad \frac{100\ D_i}{L}$$

et

$$D_i^2 = \frac{100\ D_2}{L} \qquad a_i = \frac{100\ a}{L}$$

Se rapportant respectivement à la longueur de la tête, à la position des dorsales et de l'anus.

Longueur en cm.	T_i	D_i^1	D_i^2	a_i
10 à 20	26·4	27·5	39·30	39·7
20 à 30	26·9	27·8	39·15	40·2
30 à 40	26·9	27·3	39·02	40·65
40 à 60	25·98	27·2	38·85	40·9

Ces moyennes ont été calculées sur un nombre d'exemplaires assez réduit (74).

Un plus grand nombre de mesures permettra d'indiquer des valeurs plus précises ainsi que les limites probables et les limites certaines de la moyenne vraie.

F. Etude Biométrique du Merlu.

Par

Jean le Gall.

DIVERS caractères morphologiques et physiologiques de valeur inégale, parfois douteuse, ont été étudiés dans les Rapports précités, présentés au premier "Colloque du Merlu", lors de la réunion du Comité Atlantique à Amsterdam, Octobre 1951, et la nécessité d'une méthode de travail bien définie, permettant la comparaison des résultats obtenus dans les différents laboratoires maritimes s'intéressant à cette question, s'est immédiatement imposée.

Elle a entraîné un examen critique de tous les caractères ayant été utilisés jusqu'à présent par les chercheurs; elle les a conduit à les définir avec précision, à leur donner un symbole et à présenter les résultats des observations faites sous la forme d'*indices* ou de *moyennes* également bien définis.

I. Caractères Morphologiques.

Caractères métriques.

Longueurs mesurées en millimètres entre perpendiculaires, depuis l'origine au point indiqué.

Origine des mensurations: Extrémité du museau.

LT *Longueur totale:* mesurée de l'extrémité du museau prise comme origine au milieu de la ligne joignant les extrémités de la caudale.

Lc *Longueur du corps:* mesurée de l'extrémité du museau à l'extrémité du corps (origine visible des rayons médians de la caudale).

D1 *Distance pré-primodorsalis:* mesurée du bout du museau à l'origine du rayon antérieur de la 1ère dorsale.

d^1 *Longueur de la 1ère dorsale:* mesurée de l'origine du 1er rayon de la 1ère dorsale à l'extrémité postérieure de cette dorsale.

D1p *Distance post-primodorsalis:* mesurée du bout du museau à l'extrémité postérieure de la première dorsale.

D2 *Distance pré-secundodorsalis:* mesurée du bout du museau à l'origine du 1er rayon de la 2ème dorsale.

D2p *Distance post-secundodorsalis:* mesurée du bout du museau à l'extrémité postérieure de la deuxième dorsale.

d^2 *Longueur de la deuxième dorsale:* mesurée de l'origine du 1er

rayon de la deuxième dorsale à l'extrémité postérieure de cette nageoire.

V *Distance préventrale:* mesurée de l'extrémité du museau à l'origine de la ventrale.

A *Distance préanale:* mesurée de l'extrémité du museau à l'origine du premier rayon de l'anale.

Ap *Distance postanale:* mesurée de l'extrémité du museau à l'extrémité postérieure de la nageoire anale.

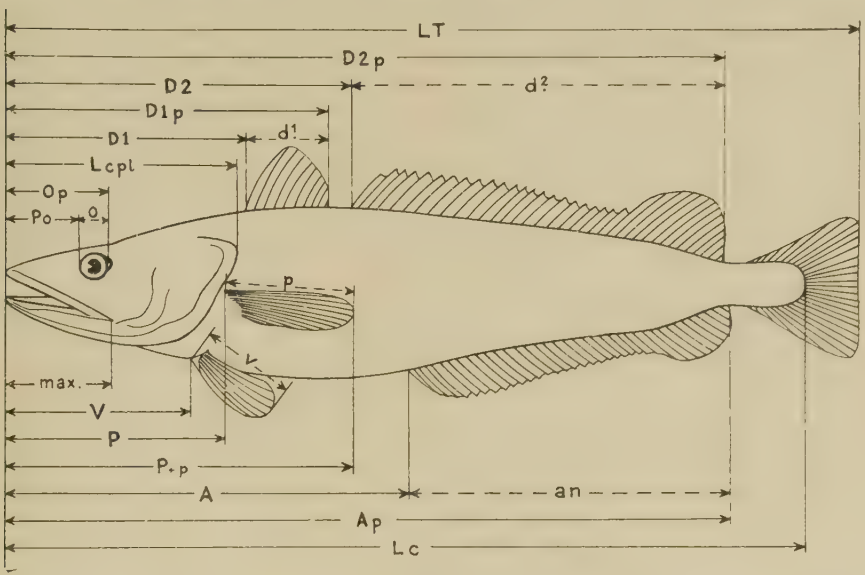

Figure 2.

an *Longueur de l'anale:* mesurée de l'origine du premier rayon de la nageoire anale à l'extrémité postérieure de cette nageoire.

P *Distance prépectorale:* mesurée de l'extrémité du museau à l'origine du 1er rayon de la nageoire pectorale.

p *Longueur de la pectorale:* mesurée de l'origine du 1er rayon de la nageoire pectorale à l'extrémité postérieure de cette nageoire.

Lcpl *Longueur de la tête:* Longueur maximum mesurée de l'extrémité du museau à l'extrémité postérieure de l'opercule.

Po *Longueur préorbitaire:* mesurée de l'extrémité du museau au bord antérieur de l'orbite.

Op *Longueur postorbitaire:* mesurée de l'extrémité du museau au bord postérieur de l'orbite.

Or *Diamètre de l'orbite:* différence Po — Op = Or.

H *Hauteur du corps:* Hauteur maximum du corps mesurée à l'aplomb du 1er rayon de la première dorsale.

Ce caractère, retenu par divers auteurs, est d'une valeur très discutable, cette hauteur variant avec l'état de plénitude de l'estomac, ainsi qu'avec le développement plus ou moins prononcé des glandes sexuelles.

Indices.

Les résultats bruts des mensurations ainsi définies, exprimés en millimètre sont à présenter sous la forme d'*indices,* calculés comparativement à une grandeur déterminée, généralement la Longueur Totale du corps, telle qu'elle a été précédemment définie, soit x/L. Pour éviter l'emploi de décimales, le résultat de cette opération sera multiplié par cent.

Les indices $I = \frac{100\ x}{LT}$ les plus importants à retenir sont:—

Lcph Indice céphalique: $\frac{100\ lcpl}{LT}$

D1i Distance pré-primodorsalis: $\frac{100\ D1}{LT}$

D2i Distance pré-secundodorsalis: $\frac{100\ D2}{LT}$

d1i Longueur première dorsale: $\frac{100\ d}{LT}$

d2i Longueur seconde dorsale: $\frac{100\ d2}{LT}$

Ai Distance préanale: $\frac{100\ A}{LT}$

ani Longueur anale: $\frac{100\ an}{LT}$

Pi Distance prépectorale: $\frac{100}{LT}$

pi Longueur pectorale: $\frac{100\ p}{LT}$

Puis, ensuite:—

Vi Distance préventrale: $\frac{100\ V}{LT}$

vi Longueur ventrale: $\frac{100\ v}{LT}$

Les valeurs: préorbitaire, postorbitaire et diamètre de l'oeil seront ramenées à la longueur céphalique:—

Oa(i) Distance préorbitaire: $\frac{100\ Oa}{lcpl}$

Op(i) Distance postorbitaire: $\frac{100\ Op}{lcpl}$

o Diamètre de l'oeil: $\frac{o}{lcpl}$

Caractères méristiques.

Ces caractères établissent la variation du nombre des pièces de quelques organes externes convenablement choisis.

Les résultats obtenus dans le dénombrement de ces pièces sont établis sous forme de *moyenne arithmétique* (m) en précisant en même temps:
— le nombre (N) d'individus examinés;
— le mode, classe de la plus grande fréquence (μ);
— la déviation standard ou indice de variabilité (σ);
— et la fluctuation probable de la moyenne (Fl.m).

Les caractères méristiques généralement retenus dans les recherches biométriques sur le merlu sont les suivants:—

le nombre des rayons des nageoires:—
RD1 Première dorsale RD1.
RD2 Deuxième dorsale RD2.
RV Ventrale, rayons dénombrés sur la nageoire gauche.
RAn Anale, 36 à 38 rayons.
RPec. Pectorale, dénombrés sur la nageoire gauche.

le nombre de branchiospines:—
Br Nettement visibles sur la branche inférieure du 1er arc branchial (arc antérieur).
Vert. le nombre de vertèbres, comptées depuis la première vertèbre cervicale située immédiatement en arrière du condyle occipital (non compté) jusqu'à la dernière vertèbre caudale, l'urostyle non compris.

Il peut être intéressant de faire la distinction entre les vertèbres cervicales, les vertèbres abdominales à arc hémal clos et les vertèbres caudales sans arc hémal.

Les caractères morphologiques à retenir.

Tous ces caractères morphologiques n'ont pas la même valeur. Les difficultés de leur évaluation ou de leur dénombrement précis, leur variabilité trop faible ou trop grande, rendent certains d'entre eux discutables.

Les experts ayant participé à leur étude et à la discussion qui la suivit, ont décidé de ne retenir parmi la liste précédente que les caractères suivants:—

Caractères métriques.
LT La longueur totale du corps, mesurée du bout du museau jusqu'au milieu de la ligne joignant les pointes de la caudale.
D1 Distance prédorsale.
D2 Distance présecundodorsalis.
V Distance préventrale.
A Distance préanale.
P Distance prépectorale.
p Longueur de la pectorale.
lcpl Longueur de la tête.
et d'établir les *indices* correspondants précédemment définis:—
I.cph — D1i — D2i — Ai — Pi — pi — Vi
Cette liste n'étant pas limitative.

Caractères méristiques.

— Le nombre de vertèbres, calculé sous forme de moyenne, ainsi qu'il l'a été précisé;
— Le nombre de branchiospines sur le premier arc branchial, établi de même;
— Le nombre de rayons à la première nageoire dorsale.

Cette liste, comme la précédente, n'étant pas limitative.

II. Caractères Physiologiques.

Il a été reconnu utile, également, de compléter la Fiche Biométrique des échantillons de merlus étudiés à une époque déterminée, par quelques-uns de leurs caractères physiologiques observés au moment de leur capture.

Etat de maturité sexuelle. La distinction sera faite entre:—

a) Les Poissons immatures n'ayant pas encore atteint leur première maturité sexuelle;
b) Les Poissons adultes, prêts à se reproduire ou l'ayant déjà fait au moins une fois.

Stades de maturité sexuelle.

La classification recommandée par Johan Hjort pour les différents stades de maturité sexuelle du hareng, étendue ultérieurement à divers Clupéidés (sardine, sprat, anchois, alose), puis au maquereau, au chinchard, ainsi qu'à d'autres poissons. (Stades de I à VII, puis VIII (1) et VIII (2), suivant la taille et le volume occupé par les glandes génitales) peut être retenue pour sa simplicité.

Cette notion sera avantageusement complétée par l'examen microscopique des organes sexuels, ainsi que par l'étude de la corrélation:

$$\frac{\text{Poids des glandes génitales}}{\text{Poids du corps (estomac vide)}}$$

Corrélation Poids/Taille (P/LT).

Le poids (P) étant calculé en grammes (estomac vidé), la longueur totale (LT) exprimée en centimètres et ramenée au centimètre inférieur.

Corrélation Taille et Age (Notion de croissance).

La taille étant exprimée en centimètres et ramenée au centimètre inférieur.

L'âge déterminé d'après le nombre d'anneaux d'hiver observés sur l'écaille ou sur l'otolithe.

Les résultats encore discutables obtenus dans cette détermination nécessiteraient l'étude comparative des observations faites sur chaque individu étudié par l'examen des écailles et celui des otolithes jusqu'à ce qu'une conclusion puisse être tirée sur la valeur de l'une ou de l'autre de ces pièces squelettiques pour la détermination de l'âge.

Letter to the Editor.

East-African Fisheries Research Laboratory,
Jinja, Uganda.
19th March 1952.

To the Editor, Journal du Conseil.

Dear Sir,

Since the publication of the paper on "Factors Influencing the Runs of Elvers in the River Bann, Northern Ireland" in the *Journal du Conseil* (Vol. XVII, No. 3, 1951, pp. 299—315) I have been informed that the records of elver catches sent to the Freshwater Biological Association in 1944 by the Northern Ireland Government for analysis, and on which this paper is based, were drastically revised by the Northern Ireland authorities in 1947. The Freshwater Biological Association was not notified of the extent of these revisions. It seems therefore that the figures on which this paper was based were much less accurate than I had reason to believe, and the conclusions reached in this paper have had to be reconsidered. As comparable data for elver runs up the River Bann between 1944—48 have now become available, and are thought to be more accurate than the 1936—43 data, these additional data have been taken into account when reconsidering these conclusions.

A full list of errata is being deposited in the Offices of the Conseil International pour l'Exploration de la Mer in Charlottenlund Slot, Charlottenlund (near Copenhagen). Discrepancies in the figures sent for analysis in 1944 and the revised "corrected" figures concern weights of elvers caught and affect the totals for each year from 1936—43. In some cases there are also differences in the days on which elvers were recorded, though the total number of "running days" per year and the dates that the first elvers were trapped each season remained the same for all the years. Contrary to earlier information that the traps "were emptied as nearly as possible each day" (see page 303), the Northern Ireland authorities now state "we record only the dates on which the traps are fished, not the date of run of the elvers, so that differences of two or three days are quite usual".

The "corrected" figures are, in my opinion, unlikely to be sufficiently accurate to justify a new detailed analysis based on the revised figures. All that can be said from the revised and new figures is:—

1. The starting date of the migration up river is still significantly later in the years with a high river discharge in March (as Figure 4) and early April (see Figure 2). The 1944—48 figures support this, the migration starting on 3rd March 1945 in the absence of floods, 9th March in 1948, 23rd March in 1944 and 1946, and being delayed until 19th April in 1947 by high floods.

2. There is a tendency for the season's total catch to be higher after a high discharge early in the season, though this tendency is not as marked as formerly believed and the season's total can no longer be related to the date of premigration floods as clearly as suggested on page 305. The rather high total catch in 1938 and low totals in 1939 and 1947 provide exceptions to this tendency; exceptions are perhaps to be expected as the number of elvers in the sea is likely to vary from year to year (see page 304). The revised figures are:—

Discharges early in the season	Low		Intermediate		High	
	Year	Total catch lb. elvers	Year	Total catch lb. elvers	Year	Total catch lb. elvers
	1943	14,085	1936	16,215	1939	14,175
	1944	11,385	1946	14,861	1942	15,345
	1945	11,748			1937	19,890
	1938	17,640			1941	21,600
					1940	18,955
					1947	10,744
Average catch per year — lb. elvers	(4 years)	13,714·5	(2 years)	15,538·0	(6 years)	16,784·8

3. Late-starting seasons tend to be short and early-starting seasons long though there is little difference in the number of "running days" from year to year.

4. The migration tends to be broken into more numerous, distinct runs in the long low-total seasons than in the short high-total years. Factors, such as high river discharge, which appear to divide the migration into distinct runs in the long low-total seasons may have proportionately less effect in the short high-total years, e.g., a comparison of runs in relation to water discharge in 1943 and 1940 (Figure 2) shows this clearly. The additional data throw new light on this, as, contrary to experience in earlier years, in 1947 a low seasonal total of elvers occurred despite floods which delayed the starting date. River discharges comparable with those of 1940 and 1943 divided the migration into distinct runs in 1947, suggesting that the number of elvers in the estuary is more important than the starting date in determining whether the migration continues or not under particular conditions (see p. 309). This supports conclusions reached from the data in Table 3 relating threshold discharges stopping the migration to the

season's total catch; the conclusions from this table still hold though the seasonal totals are all proportionately smaller.

5. The value of any consideration of the effect of other factors, such as tide and temperature, is particularly dependent on accurate recordings of daily runs. As it is now said that "differences of two or three days are quite usual" analysis concerning these factors can only be very general.

A. The effect of tide on elver runs has had to be reconsidered and the following table and observations should be substituted for Table 2 and Figure 3 and the comments on this table and figure on pages 307 and 308.

Revised Table 2.

	* Tide	1936	1937	1938	1939	1940	1941
Number of days elvers ran	Spring	25	16	27	18	21	25
	Intermediate	6	7	8	6	7	8
	Neap	15	28	25	21	22	24
Difference between springs and neaps		+10	−22	+2	−3	−1	+1
Total weight of elvers caught — lb. —	Spring	8475	4500	9450	5940	7965	9000
	Intermediate	2340	2700	2565	1800	2045	2880
	Neap	5400	12,690	5625	6435	8945	9720
Difference between springs and neaps		+3075	−8190	+3825	−495	−980	−720

	* Tide	1942	1943	1944	1945	1946	1947	Total
Number of days elvers ran	Spring	23	35	24	31	27	12	284
	Intermediate	4	4	3	7	6	9	75
	Neap	26	14	23	25	20	19	283
Difference between springs and neaps		−3	+21	+1	+6	+7	−7	+1
Total weight of elvers caught — lb. —	Spring	6120	9630	5715	6069	10,239	3013	86,116
	Intermediate	1215	720	1035	1316	1273	1526	21,415
	Neap	8010	3735	4635	4363	3349	6205	79,112
Difference between springs and neaps		−1890	+5895	+1080	+1706	+6890	−3192	+7004

* Daily range of tide: "Spring" 6·5 feet and over; "Neap" 5·5 feet and under.

These revised figures show:—

i) Runs occurred and elvers were trapped from all heights of tide. Over the twelve years considered elvers were trapped on a total of 284 days of spring tides and 283 days of neaps.

ii) The numbers trapped from springs and neaps were not greatly different, totalling 86,116 pounds from springs and 79,112 pounds from neaps over the twelve years. More elvers were trapped from springs in six out of the twelve years and in the other six from neaps.

The revised figures show, however, that both the occurrence of runs and the numbers of elvers running at springs rather than neaps tended to be greater in the early-starting seasons. Elvers tended to run more often from spring tides than neaps at the beginning and end of the seasons when relatively few elvers were running. This again suggests that the "pressure" of elvers in the estuary is important; elvers may need the stimulation of spring tides to start the migration up river unless there are large numbers preparing to move up river. Figure 3 indicated a strong tendency for more elvers to be caught from spring tides in low-total years. These low-total years were also the early-starting long seasons with many distinct runs. The revised and additional data suggest that the tendency for more elvers to be caught from spring tides agrees more closely with the starting date (probably representing an index of long seasons broken into distinct runs) than with the season's total catch. If the seasons are arranged in order of the starting date of migration, in the first six (1945, '43, '38, '44, '46, '36), runs from spring tides predominate, whereas for the second six, the late-starting seasons (1942, '39, '37, '40, '41, and 1947), more elvers were trapped from neap tides.

The effect of tide on the runs is also masked by floods. Apart from 1943 (a year with alternating floods and periods of very low river discharge: see Figure 2), more elvers ran from spring tides in seasons when the river discharge was fairly low and steady.

B. Temperature. Both starting dates and temperature dates (Figure 5) remain the same. The data given in Table 4 have the same meaning though the three totals are proportionately smaller. Thus it appears from these data that the starting data and total catch are independent of air temperatures just before and during the movement into freshwater.

In spite of considerable "corrections" of the original data and personal doubt as to the accuracy of figures revised in this way, it appears that most of the conclusions based on the original data still hold for the revised data, and the additional records for 1944—48 have supported the conclusions already published.

I am, Yours sincerely

Rosemary H. Lowe.

Reviews.

A. J. Clowes. "An Introduction to the Hydrology of South African Waters." Dept. Comm. and Industr., Fish. and Mar. Biol. Survey Div., Invest. Rep., No. 12, 42 pp., 14 figs, 20 charts. Pretoria, 1950.

Diese Hydrographie, die für Fischereibiologen gedacht ist, umfasst das Seegebiet zwischen den Breitenkreisen 20°S. und 45°S. und zwischen den Meridianen 5°W. und 45°E. Sie stützt sich ausschliesslich auf die Beobachtungen der Forschungsschiffe "Discovery" (15 Stationen), "Discovery II" (171 Stationen), und "Meteor" (32 Stationen).

Im ersten Teil der Arbeit wird die Verteilung von Temperatur und Salzgehalt ausser an der Oberfläche — dort nur auf Grund der verhältnismässig wenigen Stationsbeobachtungen — in verschiedenen besonders ausgezeichneten Kernschichten an Hand von 5 Karten beschrieben: in der Tiefe des Salzgehaltsmaximums unterhalb der Deckschicht, in der Tiefe des Salzgehaltsminimums im subantarktischen Zwischenwasser, in der Tiefe des Salzgehaltsmaximums im Tiefenwasser, und schliesslich im Bodenwasser. Der zweite Teil enthält die Charakterisierung der verschiedenen Wasserkörper auf Grund der Beziehung $S = f(t)$. Im dritten Teil werden in 10 Karten die Tiefenlagen von 5 ausgewählten Flächen gleicher Dichte und die Salzgehaltsverteilung auf diesen Flächen angegeben. Mit dieser Methode, der sogenannten isentropischen Analyse, wird versucht, die Ausbreitung der verschiedenen Wasserarten zu verfolgen. In der Deutung der Karten geht Clowes über die Zusammenfassung der bekannten Tatsachen hinaus und führt eigene Erkenntnisse an.

In einer Hinsicht stehen die Erkenntnisse im Widerspruch zu neueren Ergebnissen (G. Dietrich, 1935; A. Defant, 1941). Clowes vertritt die Auffassung, dass der Agulhasstrom bereits östlich der Agulhasbank auf etwa 22°E. sich vom afrikanischen Kontinentalabfall löst und seine Richtung von S.W. auf E. dreht. Damit bliebe der Agulhasstrom ausschliesslich auf den Indischen Ozean beschränkt und ein grosser antizyklonaler Wirbel südwestlich der Agulhasbank zwischen 38°—41°S. — also im Südatlantischen Ozean — würde zu einem isolierten Gebilde. Wiederholte Beobachtungen aus verschiedenen Jahren und aus verschiedenen Jahreszeiten deuten darauf, dass es sich um einen angenähert stationären Wirbel handeln müsste. Da in diesem Wirbelgebiet Wasser subtropisch-indischer Herkunft überwiegt, da ferner die Wirbelenergie unverständlich bleibt, wenn nicht der Agulhasstrom dazu beiträgt, wurde vom Referenten (1935) dieses Gebiet in den Agulhasstrom miteinbezogen. Dafür war es notwendig, auf dem "Meteor"-Profil, das von

Kap Agulhas nach Süden verläuft, zwischen den Stationen 137 und 136 den Agulhasstrom zu erwarten. Der grosse Stationsabstand von 90 sm. reicht nicht aus, den Strom eindeutig aus dem Profil nachzuweisen. Hydrographische Schnitte mit engabständigen Stationen, die senkrecht zum Kontinentalabfall südlich der Agulhasbank verlaufen, könnten Klärung in die unterschiedliche Auffassung von der Reichweite des Agulhasstromes bringen.

Es ist verständlich, dass die Darstellung eines Strömungssystems, das sicher zeitliche Schwankungen aufweist und an Kompliziertheit dem Golfstrom nicht nachsteht, bei der geringen Stationsdichte in den südafrikanischen Gewässern nicht frei von subjektiven Auffassungen sein kann. Die Bearbeitung von C l o w e s hat den grossen Vorzug, dass die 19 Kartenbeilagen die entsprechenden Beobachtungswerte enthalten, damit dem Leser eine eigene Stellungnahme erlauben und die Ergänzung in der Zukunft erleichtern.

G. Dietrich.

B. H. Ketchum, A. C. Redfield, and J. C. Ayers. "The Oceanography of the New York Bight." Papers in Phys. Oceanogr. and Meteor., **12**, 1, pp. 1—46, 20 figs. Cambridge and Woods Hole, Mass., 1951.

This paper is essentially concerned with estuarine oceanography. The authors set out to establish the circulation in a specified area of relatively shallow water; their quantitative evaluation of the factors involved leads to an estimate of the time of dispersal of river effluent.

Seven cruises each of about 25 stations were made in the 600 square-mile region of the New York Bight between February 1948 and January 1950. Using Nansen reversing waterbottles and also the more recently developed bathythermograph and salinity-temperature-depth recorder, the authors obtained an extensive array of data. In addition, subsequent analyses for oxygen and iron were made. The distributions of the various properties are discussed, with charts for surface conditions and vertical sections reproduced for each cruise. Seasonal variations were noticed, and a section deals with this subject.

In the discussion of the distributions, it is interesting to see the use made by the authors of the methods of classical oceanography. On each survey it was observed that the discontinuity layer caused by the difference in density of river and oceanic water had a slope. With several assumptions, the most important being that conditions do not change with time, it is possible to use the equation of geostrophic balance to evaluate the currents necessary to maintain the observed slope. On the three occasions when the calculated current was comparable with that estimated from water transport and also with the current measurements of M a r m e r, the authors suggest the validity of the "steady state" assumption. The remaining three estimates of currents are excessively high and are taken to indicate a temporary state of the water distribution. After a discussion of the wind conditions, they suggest that the river flow is the dominant factor in deciding the permanence, or otherwise, of the water circulation pattern.

The authors continue with an investigation of the transport of the mixed water through numerous sections of the Bight. The fraction of river water in any segment was found from the salinity distribution, and tables are given to show the distribution and volume of fresh water in the area. The transport of the fresh water through various sections has been evaluated and tabulated for the various cruises. The relation between fresh water present in the area and river flow is discussed, and by a combination of the above figures, the times of flushing of the region are estimated, these providing,

possibly, the climax to the paper. Although the river flow showed ninefold variation, flushing time only varied from six to ten days, and from the figures given there is certainly no evidence of correlation between the river flow and flushing time. Having established this independence, the authors suggest that tidal oscillations are responsible for the flushing of such regions.

An investigation of the distribution of iron in the region on the same lines as the above confirmed the values of flushing time, but gave a slightly higher figure in each case. A possible explanation of this small difference is given.

The paper should be of interest to all whose work deals with estuarine regions.

David Vaux.

D. J. Rochford. "Studies in Australian Estuarine Hydrology. I. Introductory and Comparative Features." Australian Journ. Mar. and Freshwater Res., Vol. **2**, No. 1, 116 pp., 70 figs., 1 pl. Melbourne, 1951.

This is one of those rare papers where the author not only presents some worthwhile ideas, but puts them to work. It is a refreshing change from the recent flood of inconclusive theoretical papers in this field, couched in the jargon of mathematical physics.

Rochford gives a detailed, and in places laborious, discussion of estuaries from the standpoint of an economic biologist interested in oyster culture. His extensive review of the methods of sea-water analyses creates the impression that he plans to discuss his observations at some length. Instead he goes on to present his conclusions on estuary régime, and its influence on biological productivity, citing only such data as are necessary for illustration. Since the obviously enormous amount of data are predigested, the reader is free to give complete attention to Rochford's ideas, which are certainly worthwhile.

Although precipitation in northern Australia occurs only in the summer (January), in the south-west only in the winter (July), and in the south-east throughout the year, attempts to classify estuaries solely on the basis of the corresponding run-off cycles were unsatisfactory. A more realistic classification results when the nature of circulation, and zones of influence of fresh and sea water are considered.

An estuary is the region from the upper limit of tidal rise in the river to the seaward limit of freshwater influence. In deep estuaries with non-turbulent tidal flow the structure and circulation are *atidal*. Here the fresh water moves persistently seaward over the persistently intruding sea water, mixing with it to a limited extent, and becoming more saline to seaward. The mixing boundary is longitudinal and the upper and deep layers are separated by a halocline, and a thermocline, and are distinct environments which tend to conserve their properties. The variation of properties during the tidal cycle at any point in the system is small.

The circulation is *tidal* when the halocline boundary between the brackish and sea water extends from surface to bottom. In this case there are series of cells in which the waters are relatively homogeneous, and the salinity of the cells grades from brackish to sea water in the length of the estuary. In tidal systems the upper and deep waters are continually re-circulated and no conservation exists. The cells advance and retreat with the tide so that there is a definite cycle of variation of properties at any point.

Both *tidal* and *atidal* systems are flushed by fresh water during freshets

and by sea water during droughts. Between these extremes there is an equilibrium stage, coincident with the mean discharge taken monthly over several years.

Tidal systems may be divided into four zones; (i) the *freshwater* zone in the river from the upper limit of tidal rise to the upper limit of sea water intrusion; (ii) the *gradient* zone in the region where there is a marked variation (conflict) of chlorinity (salinity) associated with the tide; (iii) the *tidal* zone in which there is a rise and fall of the tide, exposing mud flats, but no great diurnal chlorinity conflict; (iv) in the *marine* zone to seaward there are no tide flats and the fresh water from the estuary reaches infinite dilution in the coastal seas.

In the examination of an estuary the vertical and horizontal chlorinity structure are observed. Highly stratified systems are *atidal*, and zonation is absent or weakly developed. Where stratification is small the zones are distinct and the limits of the *freshwater* and *gradient* zones may be accurately distinguished by the intrusion of sea water, and the region of chlorinity conflict. These estuaries may be classified as *marine*, *tidal*, *gradient*, or *freshwater*, as one zone or another occupies the greatest volume.

The nature of the bottom and the speciation of the sessile biota are adapted to the zone classification, and productivity is dependent on the supply of nutrients in the fluid and solid media.

As direct estimates of plankton are lacking, the productivity of the water is based on the annual cycle of phosphates. In northern Australia the rivers flood in the summer, and presumably (since they were not examined) bring adequate phosphates to the estuaries at the time when the phosphate level in the sea is low. During the winter drought the sea water, in which phosphate level is high, intrudes the estuary and provides the necessary nutrients. Consequently, these systems should have a high productivity potential.

In south-west Australia the annual flood, carrying leached nutrients, occurs in the winter (July) and spring at the time when the marine nutrients are also at a maximum. Because of the dominance of fresh water in the estuary there is no vernal plankton bloom to fix the nutrients which are swept out to sea and lost. The marine waters are dominant and barren in the summer. Consequently, productivity is always low.

In south-east Australia the rainfall is more uniform, so the floods are small and do not appreciably displace the zones in the estuary. The nutrients leached from the land are fixed by the plankton, but the nutrient level is low and effectively limits productivity.

From the *freshwater* to the *tidal* zone, the bottom deposits grade from coarse sand and gravel to flocculent black mud, becoming increasingly rich in iron, nitrogen, and organic carbon, and are uniformly rich in adsorbed phosphorus. The release of nutrients by decaying matter in the mud is rapid and is aided by bacterial action. Their fixation in the surface layer of mud appears to be controlled by the extent to which the iron is in the ferric or ferrous state. This in turn is controlled by the redox potential which varies with the oxygen content in the phase boundary. Sub-stratum muds do not contribute to the exchange of nutrients.

The exchange of phosphates between the phases also appears to be related to the relative concentrations, since the exchange is slow when the difference is small, but rapid when it is large. This phenomenon is utilized to increase commercial oyster production by setting trays of phosphate-protein fertilizer on the beds. When the fertilizer was broadcast on the bottom a considerable amount was lost by occlusion in the mud.

R o c h f o r d is to be congratulated on this much needed régime treatment of the waters and bottoms of estuaries, in which he correlates the accepted ideas of structure and mechanism. The work may well be used as a primary reference, or even as a text. It requires considerable effort on the part of the reader because the development is somewhat obscured by the attention given to detail of methods. The reader should prepare a table of contents from the subject headings. It is unfortunate that the figures are arranged aesthetically, rather than being contiguous to their context.

John P. Tully.

V. L. Loosanoff, W. S. Miller, and **P. B. Smith.** "Growth and setting of larvae of *Venus mercenaria* in relation to temperature." Journ. Mar. Res. **10**, 1, pp. 59—81, 9 figs. New Haven, Conn., 1951.

Larvae of *Venus mercenaria* were grown from fertilized egg to settlement stage in 20-litre crocks at constant temperatures of 30, 27, 24, 21, and 18°C. ±1·0°C. Density of larvae, quantity of food, salinity, pH, and amount of light were identical in all cultures. The amount af aeration varied, but experiments showed that its effect on the rate of development and percentage survival to setting stage was negligible. The food used was a mixture of *Chlorella sp.* (ca. 300,000 per ml.) and purple sulphur bacteria *Chromatium perty* (ca. 400,000 per ml.). The water was changed every two days. The initial density of fertilized eggs was 50 per ml.; percentage survival to the setting stage was high in all experiments within the range 18—30°C.

The effect of temperature on the duration of larval life in lamellibranchs was in general confirmed. The results of four series of experiments were not fully consistent and it is believed that some obscure differences in the batches of water used were responsible. It was apparently impracticable to free the water used from all micro-organisms and it was, therefore, filtered through thick cotton. It seems that these differences in rate of development in larvae maintained under precisely similar conditions of salinity, temperature, and food supply (apart from small quantities of finer nanoplankton passing the cotton filter) may be associated with metabolites or with some as yet undetermined growth-promoting or growth-depressing substances present in variable amounts at different seasons of the year. One is reminded of D. P. W i l s o n' s recent work at Plymouth on the development of echinoderm larvae in Channel and Celtic Sea water. In both series of experiments the complete removal of all micro-organisms from the water immediately after collection would have eliminated a variable the importance of which it is at present impossible to assess.

The larvae of *Venus mercenaria* began to set as early as seven days after fertilization at 30°C. but not before 16 days at 18°C. Average periods for the high and low temperatures were approximately ten and twenty-two days. At constant temperatures of 15 and 33°C. ± 1·0°C. eggs showed abnormal development and a heavy mortality, few reaching the veliger stage.

Some experiments of great interest on the food requirements of the larvae are discussed very briefly towards the close of the paper, but the evidence on which the conclusions are based is not given. Larvae of *Venus mercenaria* were fed on detritus of two main types, derived from a plankton culture tank and shore pools respectively. It was found that growth-rate in these experiments was much inferior to that of larvae fed on the standard mixture of *Chlorella* and sulphur bacteria, and usually the detritus-fed larvae died of starvation

before setting. These particular experiments seem to have been somewhat crudely designed, but in view of the success obtained by the authors in rearing dense cultures of *Venus mercenaria*, the almost complete failure of the detritus-fed cultures is probably significant. More precise experiments of this nature, in which the detritus in some of the cultures was sterilized before being fed, might give results of great interest and importance.

It is stressed that the material used was all obtained from clams taken from one area, Long Island Sound, and no attempt has been made to investigate the possibility of the existence of physiological races of this mollusc varying in their requirements for larval development and setting.

H. A. C.

Gilbert M. Smith (edited by). "Manual of Phycology. An Introduction to the Algae and their Biology." 375 pp., 48 figs. Chronica Botanica Company, Waltham, Mass., 1951.

The present volume forms No. 27 in the new series of Plant Science Books produced by Frans Verdoorn and in general deals with work published prior to 1949. The editor has allotted a specific number of pages to each of eighteen authors, many of whom are specialists in the subjects which they discuss. The treatment of each subject has, however, been left to each author's discretion.

The first chapter, devoted to the history of phycology, by G. W. Prescott, gives a relatively detailed introduction to the historical developments prior to 1800, whereas more recent work is treated in general terms with considerable emphasis upon systematy. Following this, G. M. Smith, writing on the classification of Algae — after considering the validity of the Thallophyta concept — gives a clear, concise account of the Divisions of the algae and their possible inter-relationships. The subsequent seven chapters deal with the various Divisions; Chlorophyta by M. O. P. Iyengar, Euglenophyta by T. L. Jahn, Chrysophyta by F. E. Fritsch, Pyrrophyta by H. W. Graham, Phaeophyta by G. F. Papenfuss, Cyanophyta by F. Drouet, and the Rhodophyta by K. M. Drew. In each of these sections an adequate account is given of characteristic organisms, their occurrence, anatomical and morphological features, reproduction, and classification. Treatment varies from one Division to another, but each chapter is complete in itself, forming a comprehensive review of the subject useful both to students desiring an authoritative survey of the situation in any particular group and to research workers seeking an up-to-date account of modern views in their own and related fields. The indication of gaps in the knowledge of life-histories, as in the chapter on Phaeophyta, has a particularly stimulating effect and suggests that phycological research is in a dynamic state and that the need for further investigation is an urgent necessity.

Remaining chapters deal with fossil Algae, cytology, sexuality, pigments, physiology, and biochemistry, ecology of freshwater Algae, and ecology of marine Algae and plankton Algae; two appendices treat of methods of cultivation and microtechnique. The collection of all this information into one volume serves a most useful purpose, the result being the most comprehensive account of the algae and their biology to appear since volumes I and II of the "Structure and Reproduction of the Algae" were published in 1935 and 1945 respectively. The present volume unfortunately gives no account of the economic uses to which algal products are put, and no mention

is made of the large-scale commercial harvesting which is now undertaken in many countries. This omission is particularly regrettable since in a manual of this nature the correlation between industrial demand and the resulting stimulus to large-scale ecological surveys and experiments could well have been happily emphasized.

In several instances criticism could be levelled at the utilization of space by particular authors — thus in Appendix B, where only four-and-a-half pages are allowed for the consideration of microtechnique, space is devoted to a description of lowering a coverslip onto a slide; as a result the remaining space is too short to describe other than well proven techniques already familiar to most students. The most modern work cited in the bibliography was published in 1941, so that the recent advances in technique are not indicated.

There are indications that drastic elision has taken place in chapter 8, with the unfortunate result that after a brief introductory section dealing with general features, the author embarks upon descriptions of eight families of Cyanophyta without giving any indication of their inter-relationships or delimiting features. The possible relationship of this with other Divisions is not considered, nor is there any emphasis upon the isolation of the Cyanophyta.

Misprints are occasional and the majority unimportant, a particularly unfortunate exception being that on page 235, line 12, where "reaction 1" is referred to, although "reaction 0" appears to be intended. Bibliographies appear at the end of each chapter and vary considerably in composition — in many instances containing papers not referred to in the text and in others omitting papers which have been described in the text. Of the nineteen bibliographies in the manual only five — those of chapters 7, 8, 12, and 15, and Appendix A — are entirely free from inconsistencies with citations in the text and afford a complete and accurate list of authorities there mentioned without additions or subtractions.

Other indications of hurried proof-reading lie in the absence of lettering in the following figures:— Figure 16 I, H, S, X, Y, Z, and W, Figure 2 Y, Figure 8 I, Figure 13 J, and in the complete absence of "Fig. 2" referred to on page 76, line 44, and on page 80, line 11. The variability in spelling, such as "sulfur" and "sulphur", "carotinoids" and "carotenoids", may well be regularized in a second edition.

The present volume is likely to find widespread use among a varied population of students, teachers, and research workers and may well become one of the standard works on phycology.

Sheila Lodge.

W. C. Hodgson. "Echo-Sounding and the Pelagic Fisheries." Min. of Agric. & Fish., Fish. Invest., Ser. 2, Vol. **17**, No. 4, 25 pp., 24 figs. London, 1950.

The author sets out, with the aid of 26 excellent photographic reproductions of echo-charts, to demonstrate the use of the recording echo-sounder as a fish-locating device. After a brief historical narrative on the development of echo-sounding he deals with the subject under three headings:— (1) *the echo-chart,* in which some echo-chart defects due to mechanical factors are discussed; (2) *"searching for echoes",* in which practical hints on the echo-search technique are given; and (3) *classification of echoes,* which deals with the classification of echo-charts and their assignment to particular species of

fish. Although much useful information, particularly to the practical fisherman, is contained under headings (1) and (2), it is the section dealing with the classification of echoes which is of the greatest interest and importance.

This classification was made from echo-charts obtained during the course of the pelagic fisheries off the English coasts from Yorkshire to Cornwall, most of them being obtained with M. S. XII recording echo-sounders made by Marine Instruments Ltd., which were fitted to the research vessels operating in this region. Information as to the species of fish present under the recording vessel was obtained with the use of appropriate fishing gear. Dr. Hodgson shows that the echo-charts could be classified into well defined groups and that each type could be assigned to a particular species of fish. The types of echo-charts described are those given by shoals of herring, pilchard, sprat, mackerel, and the gadoids, cod, coalfish, and pollack. Of particular interest is the difference between herring and pilchard traces, which may be distinguished by the "hardness" of the top edges of the traces. Sprat traces are characterized by "comet-shaped" patterns, mackerel by "striations", and the gadoids by the "spotty" nature of the records.

It is very clear that these results should be of great help to those engaged in the search for fish in these areas, and all are advised to study the excellent reproductions of the types of echo-charts met with in the English fisheries. In view of the wide use to which this paper may be put by fishermen, it is important to emphasize that this classification is restricted to records obtained off the English coasts only, and that therefore it is not necessarily applicable to those obtained in other areas. In the Scottish fisheries, for instance, traces of the type shown in Figures 6 and 15, and attributed to pilchards, are of frequent occurrence, and they have been shown to be produced by herring shoals. The comet-shaped traces assigned to sprats are also frequently obtained in the deep off-shore waters of the northern North Sea.

It is not surprising that different species of fish in widely separated areas should give rise to similar echo-charts when it is realized that the trace pattern obtained for any species of fish is determined primarily by its shoaling habits. It can be shown from simple theoretical principles that compact shoals of all species of fish of approximately the same scattering cross-section, when in motion relative to the recording vessel, will give rise to a body of traces similar to those shown in Figures 6, 12, and 15. The exact form of the trace will depend upon the size of the shoal, its speed of movement relative to the vessel, its distance from the receiving oscillator, and the type of echo-sounder used. The relative speed of movement of fish shoal and vessel is of particular importance in determining the trace-pattern, and these patterns may be very different between recordings taken on a vessel steaming at 8 to 10 knots and those taken when it is drifting with wind or tide. Dr. Hodgson makes little mention of this important factor in his paper, although it is evident from the illustrations that both types of recording have been used in the echo-chart classification.

However, these comments do not invalidate the main features of the classification of echo-charts obtained in the English fisheries, since the shoaling habits of the different species of fish encountered there are sufficiently different for distinct echo-trace patterns to be recognized. Clearly, it is the duty of those engaged in the pelagic fisheries in other areas to follow Dr. Hodgson's example in determining the echo-chart pattern produced by the fish shoals found there.

B. B. Parrish.

A. E. J. Went. "Movements of Salmon around Ireland. 1. From Achill, Co. Mayo (1948—1950)." Proc. Roy. Irish Acad. **54**, B, 8, pp. 169—201, 9 figs. Dublin, 1951.

The investigation described in this paper forms part of the co-ordinated scheme of salmon tagging drawn up by the International Council for the Exploration of the Sea (Salmon and Trout Committee) at its meeting in Stockholm in 1946. The object of this scheme was to try to establish, by means of a series of investigations carried out in a number of countries throughout Europe, the routes followed by Atlantic salmon on migration from the feeding grounds in the sea to their native rivers. The plan formed a continuation and extension of similar work carried out prior to 1939 on a national scale in several countries, notably in Norway, Scotland, and Ireland.

Tagging of clean adult salmon was carried out at three stations on the Island of Achill off the west coast of Ireland during 1948, 1949, and 1950 (two stations only in 1948). A few sea trout also were tagged in the course of the operations. The site was chosen after consideration of information that was available from such sources as drift-netting in the sea, kelt tagging, and the commercial fishing by bag nets and draft nets at various points on the coast. This information is briefly reviewed in the paper, and it is interesting to note that the results of the tagging investigation under review contradicted some of the conclusions that had been drawn from the earlier information.

The results of the three years tagging are similar. Fish were recovered both north and south of the tagging station, the larger proportion (61·3 %) travelling northwards. With only four exceptions, all the fish recaptured south of the tagging stations travelled comparatively short distances, up to 80 km., but about one-third of those moving north travelled to distant waters, a small proportion to Scotland and Wales.

It is interesting to compare these results with those of similar investigations carried out on the west coast of Scotland (Menzies, 1936—38). From a tagging station on the coast of Ardnamurchan, salmon made long-distance migration both south and north in approximately equal proportions. From a station further north on the Island of Soay, the movement was almost exclusively to distant waters on the north and east coasts, very few recaptures being made locally. From stations still further north, at Stoer Point and Loch Inchard, only a small number of fish tagged moved south and none of these to any considerable distance, the majority making their way round the north to the east coast; one, indeed, crossed the North Sea and was recaptured at Sognefjord in Norway.

The Irish results reported in this paper, as well as the earlier Scottish results, strongly suggest that fish returning from their sea feeding grounds strike the coast at certain points — in this case the Island of Achill — where they separate out and move to their native rivers, some near the point of landfall and others at comparatively great distances. These points of landfall usually coincide with known productive fisheries.

The recorded rates of travel, up to 53 km. per day, are of the same order as those reported in similar investigations previously undertaken in Scotland and Norway. An interesting observation made during the investigation was that on several occasions fish tagged on the same day were recaptured, after travelling considerable distances, either in the same river or within a short distance of one another, suggesting the shoaling together of fish travelling to the same river.

The paper supplies another chapter in the complicated story of the

migration of Atlantic salmon. The author and his associates are to be congratulated on the successful completion of an investigation of a kind that, in the reviewer's experience, is invariably attended by practical difficulties that are not obvious from reading the finished report. Special mention should also be made of the wealth of detailed information given in the tables appended to the report, adding greatly to its value for reference purposes.

P. R. C. Macfarlane.

Gunnar Alm. "The Sea-Trout Population in the Åva Stream." Inst. Freshwater Res. Drottningholm. Rep. No. 31, pp. 26—56, 3 figs. Lund, 1950.

As the author states, many investigators have studied the sea trout in regard to such matters as seasonal migrations in various waters, and the average size, age, and rate of growth in different environments, but hitherto no comprehensive investigations have been undertaken of a particular population of sea trout over a prolonged period, or of the variations in different year-classes and their causative factors. In 1926 the opportunity was presented to the author to carry out such a long-term investigation on the Åva Stream. This involved the construction of a fish-trap for counting all upstream and downstream migrants, but it was found that the practical difficulties arising from floods and other exigencies made it impossible to carry out the research as originally planned. In consequence, it was unfortunately necessary to abandon the intention to determine, by means of direct counts, the number of smolts produced by a known adult stock and of the number of these smolts that survived to return from the sea, and also to compare the results of natural spawning and of artificial propagation respectively. In spite of this, however, the paper is an interesting and informative account of the results obtained up to 1949.

The part of the Åva Stream available to sea trout is only 2·5 km. long and varies in width between 1 and 2 metres. While the small size of the stream enabled a very detailed study to be made of the sea trout population, it also makes it necessary to exercise considerable caution in applying the results to larger rivers. As is generally found in small streams of this nature, the sea trout do not ascend until late autumn and then only for the purpose of spawning; there is no evidence of any appreciable number entering the stream for over-wintering without spawning.

The report discloses that for this particular stream, the limited amount of spawning ground available and competition for the restricted food supply were the critical factors affecting productivity; numerically rich spawning stocks invariably produced poor year-classes. It is doubtful if these results are of general application, particularly where less restricted waters are concerned, although it is common experience among both salmon and sea trout that an abundant spawning population is not invariably followed by abundance in the progeny resulting from it.

In the course of the investigation, a large quantity of scale material was collected for the purpose of determining age and growth. The age at smolt migration varied from one to five years, the majority (68·6 %) being two years old. In this respect, as in average length at migration and rate of growth during sea life, these sea trout are not unusual; but as regards age at maturity, particularly of females, they are undoubtedly later than are normally found in Scottish waters.

Tags were attached to some 2,000 adults and 500 "young fish" (presumably smolts). The merits of different tagging positions were investigated by attaching tags to the dorsal fin, the adipose fin, and the mandible. The results of recaptures disclosed that mandibular tagging was definitely inferior and that the best returns were obtained from trout tagged at the dorsal fin. The proportion of trout recaptured showing scars of lost tags is surprisingly high, but this, to some extent, is explained by the author's admission that, on occasion, the work had to be carried out less carefully than was desirable.

It is to be hoped that this interesting paper may be regarded as an interim report on the sea trout stock of this stream, and that the author may yet find it possible to renew and complete the parts of the investigation which had to be abandoned, as these concern highly important matters on which very little factual information is yet available.

P. R. C. Macfarlane.

Current Bibliography.

Prepared by the Editor with the Assistance of Mr. A. C. Simpson.

NOTE. The scope of the Bibliography is limited in the main to the area covered by the Council's activities, but there are included papers of general interest relating to other areas in North Temperate and Arctic regions and exceptionally elsewhere. Limnological references are not as a rule given, but papers relating to brackish waters and to salmon and freshwater fish studied by the Council are included.

Subscribers and those on the distribution list will receive regularly upon application to the General Secretary copies of the Bibliography printed on one side of the page only, for use in making up card indices.

The Editor will be glad to be advised of emendations and additions to the Bibliography.

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